

A Book Chapter:

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Abstract

The chapter clarifies the hormonal mechanisms that regulate wood formation in plants focusing on hardwood trees. Uncovering the specific role of each of the hormones: auxin, gibberellin and cytokinin in controlling vascular differentiation. Explaining the hormonal control of vessels and fibers along the plant axis from leaves to roots, and during the growth season. Clarifying how the environment, by controlling plant growth and dimensions, regulates the internal hormonal mechanisms that shape the rate of vessel widening and their final size. How the environment has modified the sensitivity of the cambium to the auxin signal during the evolution of ring-porous trees, resulting in their typical very wide earlywood vessels, followed by latewood fibers with thick secondary walls.

Keywords

Auxin

Cambium sensitivity

Cytokinin

Earlywood vessel differentiation

Environmental adaptation

Gibberellin

Latewood fibers

Pattern formation

Plant evolution

Ring-porous wood

1. Introduction

This chapter provides an overview of the internal hormonal mechanisms that control and regulate xylem differentiation in plants, focusing on wood formation in trees, clarifying the evolution and specialization of these mechanisms in temperate deciduous hardwood trees. Special attention is paid to explain a major topic in xylogenesis, namely, the control of vessel size within the whole tree as affected by external and internal factors, evolving the ring-porous wood pattern under extreme environmental conditions during the recent 50 million years.

In order to explain the evolution of ring-porous trees, I provide a summary of the three major hormonal signals that regulate wood formation for those unfamiliar with the subject and as a preamble to a discussion on the control of vessels and fibers in forest trees. Then, I focus on three major topics in vascular differentiation and the recent advances made in each, demonstrating the gradual conceptual evolution of ideas as a natural process, by presenting three hypotheses that stem from each other: (i) the control of vessel width and density along the tree axis (auxin gradient hypothesis), (ii) environmental adaptation of the xylem in plants (vascular adaptation hypothesis), and (iii) the evolution of ring-porous wood in temperate deciduous hardwood trees (limited-growth hypothesis).

2. The Conducting and Supporting Cells in the Wood of Angiosperms

The wood of plants is produced by the meristematic vascular cambium and is termed secondary xylem. Its main function is water transport from roots to leaves and the support of the plant body. Two conductive water conduits are found in wood, the tracheids which are typical to conifers and vessels that are dominant in angiosperms. A tracheid is usually a long water-conducting conduit that has no perforations. A vessel is a long tube build of vessel elements, that their common walls have perforations. The vessel is therefore a more efficient conduit than a tracheid, since water flow through vessel elements occurs via openings, namely, perforations, rather than diffusion through the primary cell walls, through the bordered pits of tracheids (Tyree and Zimmermann 2002).

A vessel has endings walls in the lower and upper ends (Aloni 2021). Transport of water from vessel to vessel occurs through pits along their vessel elements or their end cell wall. It should be noted, that vessels and not vessel elements are the physiologically operating units of water transport regarding cavitation and embolism (Zimmermann 1983; Zhang et al. 2018). Embolism of a large vessel is usually followed by the outgrowths of the surrounding parenchyma cells into the vessel, a phenomenon known as tyloses (Zimmermann 1983), which forms blockages to penetration and movement of fungi and bacteria into and along the air-filled nonfunctional vessel. There are species that gum may plug the air-filled vessel to prevent possible penetration damage. Tyloses and gum plugs develop naturally in hardwood trees when the functional water transporting sapwood gradually turns into a stable heartwood that is resistant to rot (De Micco et al. 2016).

There is a positive correlation between conductive efficiency and vulnerability to water stress and freezing inducing embolism. Wide and long vessels that are efficient conduits are more vulnerable to cavitation and embolism induced by freezing and water stresses than narrow vessels and tracheids. The widest earlywood vessels of ring-porous trees (see below) operate for a relatively short duration, usually for only one growth season and become nonfunctional at the end of the season. On the other hand, tracheids and narrow vessels are safe conduits that function for long periods of a few years, but are less efficient in water transport (Tyree and Sperry 1989; Tyree and Ewers 1991).

The vessels are accompanied by xylem parenchyma cells and fibers. A fiber in the xylem and phloem is usually a long cell characterized by thick and hard lignified secondary cell walls with simple pits. The latter provides the mechanical strength for supporting the plant body. During evolution, both xylem fibers and vessels, have originated from tracheids of more primitive plants (Bailey and Tupper 1918; Evert and Eichhorn 2013; Aloni 2021).

2.1. The Importance of Vessel Width for Water Conductance

The hydraulic performance of trees is crucially affected by vessel diameter (Tyree and Zimmermann 2002; Lucas et al. 2013; Hacke et al. 2017; Williams et al. 2019; Olson et al. 2021; Aloni 2021), which also affects wood adaptation (Aloni 1987, 2015) and xylem pathology (Aloni and Ullrich 2008; Ullrich et al. 2019). Therefore, it is important to understand and clarify the mechanisms that control the diameter of these vascular conduits in plants.

Vessel diameter has a very important functional significance in water conduction. In ideal capillaries, conductivity is proportional to the fourth power of the radius, or diameter (Zimmermann 1983), which means that at a given pressure gradient the relative volumes of water flowing through capillaries, or vessels, of diameters: 1, 2, 3, 4, and 5, are: 1, 16, 81, 256, and 625, respectively. A cross section of a ring-porous wood demonstrates that most of the water would have flown through the very wide earlywood vessels, whereas the narrow latewood vessels would be inefficient in water conductance (Fig. 1). Yet, the narrow latewood vessels are important for plant survival as they continue to function when the wide earlywood vessels stop functioning, following cavitation and embolism.

Fig. 1 Transverse sections showing the borderline and transition from the latewood (down) to earlywood (up), in the diffuse-porous wood of *Acer rubrum* (a), in comparison with the ring-porous wood of *Robinia pseudoacacia* (b), analyzed during winter dormancy, stained with safranin and fast green. In both photomicrographs, earlywood vessels are marked by V, latewood vessels are marked with an arrow, and latewood fibers with an arrowhead. Both micrographs are at the same orientation and magnification (scale bars = 500 μm). A, the diffuse-porous wood shows functional open vessels with relatively similar width forming a continuous pattern, which was induced by the continuous production of auxin-producing young leaves along the growth season. The vessels of the new year are wider than those of the previous season due to the increased distance of the new year's leaves from the transverse-section site. The earlywood fibers have thin secondary walls, while the latewood fibers (arrowhead) have somewhat thicker secondary cell walls associated with narrow vessels (arrow) due to leaf maturation, which promoted gibberellin production toward the end of the growth season. B, the very wide and vulnerable earlywood vessels (V) in the ring-porous wood are already plugged by tyloses at the end of the growth season. These wide vessels were induced by extremely low-auxin-concentration streams originating in dormant looking buds, in a slow widening process along a few weeks, which started before bud break. Whereas, the latewood of the previous year contains the narrow functioning latewood vessels (arrow) that would transport water for more than one growth season. The ring-porous latewood is also characterized by numerous latewood fibers with very thick lignified secondary cell walls. Both, the safe narrow latewood vessels and thick-wall fibers were induced by the gibberellin-producing mature leaves. (see the figure at the end)

2.2. The Problem of Wide Earlywood Vessel Formation in Temperate Deciduous Hardwood Trees

In temperate deciduous broad-leaved trees, the size differences of the vessels in the early- and latewoods are quite marked and two categories of deciduous trees are determined: diffuse-porous species and ring-porous species (Fig. 1). In diffuse-porous wood the vessels produced along the season are more or less uniform in size, whereas in ring-porous wood the vessels produced at the beginning of the growth season are significantly wider than those produced at the end of the season (Evert 2006; Aloni 2021).

Although Hartig (1853) and Russow (1883) observed long ago the formation of wide vessels in the trunk of *Quercus* trees at the very early stage of bud development, the mechanisms that regulate the differentiation of wide earlywood vessels in temperate deciduous ring-porous trees still need clarifications (Suzuki et al. 1996; Sass-Klaassen et al. 2011; Takahashi et al. 2013; Pérez-de-Lis et al. 2016; Lavrič et al. 2017; Puchařka et al. 2017; Rodriguez-Zaccaro et al. 2019; Zhu et al. 2020). Interestingly, ring-porous species produce diffuse-porous xylem in their young leader, twigs and branches during their first year, while they produce the typical ring-porous xylem along their mature trunk (Cochard & Tyree, 1990; Lo Gullo et al. 1995; Takahashi et al. 2013; Rodriguez-Zaccaro et al. 2019); these differences between the two types of wood porosity produced along the same ring-porous tree were recently elucidated (Aloni 2021) and will be discussed below. Additionally, it is unclear how the regulating mechanisms of wide earlywood vessel formation are influenced by climatic factors in different hardwood trees in temperate forests (Sass-Klaassen et al. 2011; Pérez-de-Lis et al. 2016, 2018; Hacke et al. 2017; Gričar et al. 2018, 2020; Zhu et al. 2020).

In ring-porous species, the first earlywood vessels are very wide and are formed at, or just prior to, the breaking of buds. Conversely, in diffuse-porous trees the earlywood vessels are formed much later and appear in the trunk when the leaves are one-fourth to fully expended (Lodewick 1928). Furthermore, in ring-porous trees the initial wide vessels develop almost simultaneously all along the main stem (Atkinson and Denne 1988), whereas in a diffuse-porous tree they are restricted to the base of the buds, appearing first in the lower branches and later in the upper ones (Atkinson and Denne 1987). The wide earlywood vessels in ring-porous trees are also very long and can extend along the length of the stem itself (Greenidge 1952; Zimmermann and Jeje 1981), whereas the earlywood vessels of diffuse-porous species are narrow and much shorter, usually less than 1 m (Zimmermann and Jeje 1981).

When young trees are completely debudded in late winter, before any bud activity can be observed, new earlywood vessels differentiate in ring-porous trees, but are entirely absent in diffuse-porous species (Wareing 1951; Reines 1959). Young growing leaves are known to produce the auxin hormone that moves downward and induces cambial cell divisions and the differentiation of vessels along its pathway (Snow 1935; Jacobs 1952; Sachs 1981; Aloni 1987; Scarpella and Helariutta 2010). Therefore, it was difficult to explain the cambial reactivation and wide earlywood vessel differentiation in both normal and debudded ring-porous trees. Wareing (1951, 1958) suggested that in the cambium of ring-porous trees there is a high initial reserve of an auxin precursor that enables early cambium reactivation and rapid spread of earlywood vessel formation at an early stage of bud development. Presumably, in ring-porous species this reserve of auxin is accumulated during the previous season, whereas in diffuse-porous species little or no such reserve is formed. Wareing also hypothesized that the very wide earlywood vessels of ring-porous trees are induced by high supply of auxin in spring (Wareing 1951, 1958; Digby and Wareing 1966). However, results that contradict Wareing hypothesis were obtained in experiments on ring-porous trees (Aloni 1991), showing that application of moderate or high auxin concentrations to debudded trees, before bud

break, inhibited the formation of wide earlywood vessels and yielded narrow vessels in the earlywood, and will be discussed below. These contradicting results point out a need for a new general hypothesis to solve the problem of how the wide earlywood vessels are induced, and account for the fundamental differences in wood porosity between ring-porous and diffuse-porous species, which will be clarified in this review.

3. The Three Major Hormonal Signals that Regulate Wood Formation

The major signaling molecules that regulate vascular differentiation and plant development are the plant hormones, also called phytohormones (Went and Thimann 1937). The hormones can be produced in any living plant cell at extremely low concentrations. They may act locally or at a distance from the producing cells.

Very few phytohormonal signals enable regulation and adaptation in remarkably simple mechanisms. The developmental process could be carried out by either a single developmental signal, or by very limited number of signals. The use of one or two signals is an economical way for carrying out major integrating roles.

The three primary phytohormonal signals that control vascular differentiation are: auxin, gibberellin, and cytokinin. Additional hormonal signals may be involved in specific responses to the environment, various stresses, wounding, and regulation of specific cell differentiation. The role of the hormonal signals and their molecular mechanisms in vascular differentiation were extensively reviewed in recent years by Caño-Delgado et al. (2010), Scarpella and Helariutta (2010), Lucas et al. (2013), Aloni (2013a, 2015), Furuta et al. (2014), Zhang et al. (2014), De Rybel et al. (2016), Scarpella (2017), Hellmann et al. (2018), Taiz et al. 2018; Fukuda and Ohashi-Ito (2019), Agustí and Blázquez (2020), and Aloni (2021).

All these three primary hormones are moving signals that are transported in specific pathways through the primary (originate from procambium) and secondary (originate from cambium) vascular tissues (Aloni 2010, 2015, 2021). In addition, hormonal movement through young parenchyma cells can induce regenerative differentiation (Jacobs 1952; Sachs 1981; Aloni 2021).

Auxin is the young leaf signal (Jacobs 1952; Sachs 1981; Aloni et al. 2003), gibberellin is the mature leaf signal (Dayan et al. 2012), and cytokinin is the root cup signal (Aloni et al. 2004, 2005). The continuous flow of these hormonal signals enables the plant to continuously respond to changing environmental cues.

The three hormonal signals are mainly produced by different plant organs and thus informing the stem cells of the embryonic vascular cambium, through which they move, on the physiological strength and quantity of the producing organs and their developmental stage. The vascular tissues are induced and regulated accordingly and the produced vascular elements reflect the developmental phase and amount of the plant organs. Thus, for example, during early spring when there are mainly young leaves on the stem of a hardwood tree, the auxin they produce is the main signal flowing through the cambium which, therefore, produces mainly sieve tubes and vessels; while during late summer when there are mainly mature leaves building large foliage biomass, their produced gibberellin becomes the dominant signal resulting in the formation of numerous fibers building stronger wood, which supports the enlarged shoot. Leaf development and biomass are regulated by environmental conditions (i.e., photoperiod, water availability, temperature, and

nutrients), which control the production of wood and the type, quantity and patterns of its differentiating vascular cell.

Understanding the role of each hormonal signal is the key to understand how these moving signals design plant development, structure and vascular tissue differentiation under different environmental conditions.

3.1. Auxin (IAA) from Young Leaves Induces Vessel Differentiation

Developing buds and young growing leaves synthesize the auxin hormone, namely, indole-3-acetic acid (IAA), which is primarily produced in the hydathodes (Aloni 2001; Aloni et al. 2003; Baylis et al. 2013; Yagi et al. 2021), moves polarly downward to the root tips and induces vessels along the auxin pathways (Jacobs 1952; Sachs 1981; Aloni 2010, 2021). Auxin is a limiting factor for vessel differentiation, in its absence there is no vessel development. The polar auxin movement from the young leaves to the roots, which induces the vessels occurs through the procambium, parenchyma cells and cambium. Auxin stimulates cambial reactivation in spring and induces earlywood vessel formation along the cambium (Aloni 1991). The polar movement of IAA is continuous, ensuring the formation of continuous vessels, which transport water from root to leaves. Wounding that interrupt the auxin flow, results in bypasses of new auxin streams that induce vessel regeneration around the injury (Jacobs 1952; Sachs 1981; Berleth et al. 2000; Scarpella and Helariutta 2010; Aloni 2021).

3.2. Cytokinin (CK) from Root Tips Promotes Cambium Sensitivity and Vascularization

Roots do not induce wood formation nor must they be present in order to form xylem in stem tissues. However, the root apices, specifically the root caps, are sources of cytokinin that promotes cambial activity (cell division) and vessel differentiation (Aloni et al. 2005, 2006; Matsumoto-Kitano et al. 2008; Nieminen et al. 2008). Cytokinins from the root tips increase the sensitivity of the cambium to the auxin signal originating in young leaves (Baum et al. 1991; Aloni 1993, 1995; Aloni et al. 2003). Cytokinin prevents the usually rapid occurring IAA conjugation (Coenen and Lomax 1997), therefore, elevated CK concentration enables the transport of extremely low-IAA concentrations via the cambium, which may explain the increased sensitivity of the cambium to the auxin hormone. Experimental evidence from transformed plants (Zhang et al. 1995; Eklöf et al. 1997) supports the idea that reduced auxin concentrations can elevate cytokinin concentration, which would enhance tissue sensitivity to the auxin signal (Trewavas 1983; Aloni 1991; Bradford and Trewavas 1994; Barbez et al. 2012). The experiments demonstrate that auxin or cytokinin modify the content of the other hormone by affecting its rate of synthesis. Reduced IAA concentration increases free CK level (Palni et al. 1988; Zhang et al. 1995; Eklöf et al. 1997). Elevated CK enhances cambium sensitivity to extremely low-concentration-IAA streams originating in swelling buds and creates the special physiological conditions that enable slow vessel widening until secondary wall deposition, resulting in the wide earlywood vessels of ring-porous trees (Aloni 1991, 2001, 2021).

3.3. Gibberellin (GA) from Mature Leaves Induces Fiber Differentiation

Mature leaves are major sources of gibberellin (Hess and Sachs 1972; Aloni 1979; Dayan et al. 2012). The GA is the specific hormonal signal that induces fiber differentiation (Aloni 1979; Dayan et al.

2012). The transport of GA along the plant axis is not polar; therefore, GA induces fiber formation in both above and below the producing leaves (Dayan et al. 2012; Aloni 2021). The bioactive gibberellins (GA1 and GA4) were predominantly found in the expansion zone of differentiating secondary xylem cells in *Populus*, suggesting that the role of GA in early stages of wood formation, is promoting cell elongation (Israelsson et al. 2005). GA, which promotes cambial activity, reduces vessel width, resulting in narrow vessels in the latewood (Aloni 2021). Ring-porous trees develop auxin-producing young leaves in the beginning of the growth season; but during most of the season they have mainly mature leaves (Aloni et al. 1997), therefore the wood of ring-porous trees is characterized by numerous hard lignified latewood fibers and narrow vessels, both are regulated by the GA originating in their mature leaves.

4. Control of Vessel Size and Density Along the Tree Axis

A well-documented phenomenon is the downward gradual and continuous increase in vessel size from leaves to roots. This widening in vessel diameter was found along leaves from the tip to the base of the leaf (Colbert and Evert 1982; Russell and Evert 1982; Lechthaler et al. 2019). A continuous gradual increase in vessel diameter and vessel length was demonstrated from twigs to branches, downward along the stem and into the roots of *Acer rubrum* trees (Zimmermann and Potter 1982). Vessels are narrow at the leaves and their diameter increases gradually downward and continuously along the stem (Carlquist 1975; Zimmermann 1983; Aloni and Zimmermann 1983; Sorce et al. 2013; Lazzarin et al. 2016; Williams et al. 2019; Olson et al. 2021; Aloni 2021) and the root (Riedl 1937; Fahn 1964). Whereas vessel density decreases from leaves to roots, as was found in many plant species (Fegel 1941; Carlquist 1976; Aloni and Zimmermann 1983; Leitch 2001; Sorce et al. 2013; Zhao 2015).

Although Olson et al. (2021) suspect that the increase in vessel width from leaves to roots is an adaptation of trees to their environment, the picture that they present is incomplete because they do not consider the biological causing factors, namely, the hormonal mechanisms that control vessel widening from leaves to roots and adjust plants to their environment (Aloni 2013b, 2015, 2021; Agustí and Blázquez 2020). These hormonal mechanisms provide the answers to the questions raised by Olson et al. (2021), and will be clarified below.

To explain the mechanism that controls the general increase in vessel width and decrease in vessel density from leaves to roots, Aloni and Zimmermann (1983) proposed the auxin gradient hypothesis (that was first called the six-point hypothesis) suggesting that the polar transport of the auxin hormone from leaves to roots is the morphogenetic signal that creates a gradual polar gradient in the vascular cambium along the plant axis providing directional and location information to the differentiating cells (i.e., vessels, tracheids, fibers and sieve tubes) along the morphogenetic field.

The hypothesis proposes that the final size of a conduit is determined by the rate of cell differentiation. Since cell expansion ceases after the secondary wall is deposited, high-auxin concentrations near the young leaves induce narrow vessels, because of their rapid differentiation, allowing only limited time for cell widening. Conversely, further down, low-auxin concentrations result in slow differentiation, which permits more cell expansion before secondary wall deposition and therefore results in wide vessels at the base of the stem.

Vessel density is controlled by, and positively correlates with auxin concentration; consequently high-IAA concentrations (near the auxin producing young leaves) induce great vessel density, while

low-IAA concentrations (further down, towards the roots) diminish density. Consequently, vessel density decreases from leaves to roots.

The auxin gradient hypothesis was experimentally confirmed by showing that various auxin concentrations applied to decapitated stems induce substantial gradients of increasing vessel diameter and decreasing vessel density from the auxin source towards the roots. High-auxin concentration yielded numerous vessels that remained narrow because of their rapid differentiation; low-auxin concentration resulted in slow differentiation and therefore in fewer and wider vessels (Fig. 2) (Aloni and Zimmermann 1983).

Fig. 2 Effects of applied auxin concentration (0.03% NAA, 0.1% NAA, or 1.0% NAA w/w in lanolin, renewed every 3 days) on secondary vessel differentiation in the second internode above the cotyledons of *Phaseolus vulgaris*, observed after 3 weeks of hormonal applications, on the top of the internode after the shoot above it was excised. a Effect of distance (0.5 and 4.0 cm) from 0.1% NAA application site on the rate of secondary vessel formation, showing intensive vessel differentiation near (0.5 cm) the site of auxin application. b Effect of 0.03% and 1.0% NAA on the radial diameter of the late-formed secondary vessels, along the studied internode, showing the substantial increase in vessel diameter with increasing distance from the applied auxin. c Effect of 0.03% and 1.0% NAA on the number of secondary vessels induced along a xylem radius, as affected by distance from the auxin source. Vertical bars indicate standard errors which are comparable at all points (from Aloni and Zimmermann 1983)

Studies on transgenic plants with altered levels of auxin confirmed the general relations between IAA concentration and vessel size and density. Thus, auxin over-producing plants (i.e., over-expressing the *iaaM* gene) contained many more vessel elements than did control plants, and their vessels were narrow (Klee et al. 1987); conversely, plants with lowered IAA levels (i.e., expressing the *iaaL* gene as an anti-auxin gene) contained fewer vessels of generally larger size (Romano et al. 1991).

A recent study of conduit diameter in the earth's tallest tree species: *Eucalyptus regnans*, *Sequoia sempervirens*, and *Sequoiadendron giganteum*, that were 86–105 m tall and exceeded 85% of the maximum height for each species, showed the typical gradual increase in conduit width along the upper parts of their shoots. However, at the base of their trunks, below about 60 m from the tree tops, vessel and tracheid diameters approached their maximum size, as they did not continue to expand; demonstrating that at the base of these giant trees, there is a limitation to conduit widening (Williams et al. 2019).

In spring, the first very wide earlywood vessels in temperate deciduous ring-porous trees initiate a few weeks before the onset of leaf expansion (Suzuki et al. 1996; Sass-Klaassen et al. 2011; Takahashi et al. 2013; Lavrič et al. 2017; Puchałka et al. 2017; Gričar et al. 2020). The width of these wide earlywood vessels increases slowly along a few weeks, because it is stimulated and induced by low-level streams of auxin produced by dormant looking buds, before swelling. This slow vessel widening can occur only because the cambium of ring-porous trees has become very sensitive to low-IAA concentrations, as will be explained below.

5. Adaptation of the Xylem to the Tree's Environment

Vascular plants grow in different environments, ranging from deserts to rain forests and from arctic regions to the tropics. Comparative anatomical studies (e.g., Baas and Carlquist 1985; De Micco et al. 2008; Wheeler and Baas 2019) reveal similarities in structure of the vascular system in plants grown in extreme habitats versus ones grown in favorable environments. Desert (Carlquist and Hoekman 1985; Fahn et al. 1986), arctic, and alpine shrubs (Carlquist 1975) are characterized by very narrow vessels in high density. Such vascular systems are considered adaptive safety mechanisms against drought and freezing (Baas et al. 2004; Lucas et al. 2013). Conversely, forest trees and lianas, which characterize the tropics and rain forests, have low density vessels of very wide diameter at the base of their stems (Carlquist 1975; Zimmermann 1983; Ewers 1985; Tyree and Sperry 1989), which affords maximal efficiency of water conduction (Ellmore and Ewers 1985; Tyree and Ewers 1991; Tyree and Zimmermann 2002; Olson et al. 2021) and is considered to be an adaptation to mesic conditions.

In order to explain the adaptation of plants' vascular systems to the environment, Aloni (1987) proposed the vascular adaptation hypothesis suggesting that the environment controls the plant's vascular system through its control of plant's development, height, and shape. Limiting conditions suppress plant growth and shorten the active growth period, which restrict plant development resulting in small plants. Conversely, favorable conditions allow growth activity throughout the year, enabling more growth and consequently well-developed plants and maximal height.

The height of the plant and the degree of its branching determine gradients of auxin along the plant's axis. In small shrubs, which are typical to extreme stressful environmental conditions, the distances from the young leaves to the roots are very short and no substantial decreasing gradient of auxin can be formed. Therefore, the concentrations of IAA along these small plants are relatively high and result in rapid differentiation of numerous very narrow vessels in the greatest densities (as predicted by the auxin gradient hypothesis, Aloni and Zimmermann 1983). Conversely, in large trees and in long lianas, the very great distances from the young auxin-producing leaves to the roots enable a substantial decrease in auxin concentrations in their lower parts, leads to slow conduit differentiation that allows more cell expansion before secondary wall deposition, resulting in very wide vessels in low density at their base.

The vascular adaptation hypothesis (Aloni 1987) was confirmed experimentally (Aloni 1988, 2021) and by analysing the correlation between plant size and vessel diameter on a large scale of collected species from a wide range of growth conditions (Olson and Rosell 2013). Finally, the hypothesis explains why a tree that grows in very limited conditions will produce numerous narrow vessels in high density, in comparison with a tree of the same species that develops under favorable conditions and will produce wide vessels in low density at its base.

6. Evolution of Ring-Porous Wood in Temperate Deciduous Hardwood Trees

6.1. The Limited-Growth Hypothesis

In temperate deciduous broad-leaved trees, the size differences of vessels in the earlywood and latewood are quite marked and two main xylem categories can be distinguished: diffuse-porous wood and ring-porous wood. In diffuse-porous wood the vessels are more or less uniform in size (Fig. 1a), whereas in ring-porous wood the vessels produced at the beginning of the growth season are significantly wider (Fig. 1b) than those produced at the end of the season (Evert 2006; Aloni 2021). Earlywood vessels in ring-porous trees can be huge (width of up to 500 μm and length of the entire tree) and therefore are very efficient in water conductance, but their size makes them

vulnerable. The wide earlywood vessels usually function during one season and then they become occluded by tyloses, or gum to plug the air-filled vessel and prevent possible penetration damage of pathogenic bacteria and fungi (Aloni et al. 1997; Tyree and Zimmermann 2002; Evert 2006; Aloni 2021). Tyloses formation in earlywood vessels occurs earlier under drier conditions (Pérez-de-Lis et al. 2018). When tree species that have already developed ring-porosity during evolution grow under favourable conditions, they can reach large sizes, although they usually show a slow growth pattern in comparison with faster growing diffuse-porous trees.

The challenge to understand the mechanisms that have shaped earlywood vessel patterns during the evolution of temperate deciduous hardwood trees requires elucidation of the roles of tissue sensitivity to auxin (Trewavas 1983; Bradford and Trewavas 1994; Barbez et al. 2012) and the specific hormonal signalling in these trees (Aloni 1991, 2001, 2013a, 2021). It has been suggested that ring-porous trees have originated from diffuse-porous species (Aloni 1991; Wheeler and Baas 1991). The development of ring porosity has probably arisen independently multiple times during the diversification of angiosperms, and different lineages might therefore have modified mechanisms in different families.

To explain how ring-porous wood has developed during the evolution of temperate deciduous hardwood trees, Aloni (1991) proposed the limited-growth hypothesis, suggesting that during the evolution of temperate deciduous hardwood trees, the ring-porous species have developed from diffuse-porous species under selective pressures in limiting environments, which resulted in limited vegetative growth. It was further postulated that under extreme environmental conditions the selection for ring-porous wood has led to a decrease in the intensity of vegetative growth and reduced foliar biomass, causing a decrease in auxin levels. The latter promoted an increase in cytokinin levels, which induced an increase in the sensitivity of the cambium to extremely low-concentration-auxin streams originating in swelling buds. These changes created the unique physiological conditions that enable slow vessel differentiation, which promotes a long widening process, starting before bud break, resulting in wide earlywood vessels at the beginning of the growth season (Aloni 1991).

6.2. Supporting Evidence for the Limited Growth Hypothesis

Evidence that supports the limited growth hypothesis comes from observations that a diffuse-porous tree (*Populus euphratica*) and a ring-porous tree (*Quercus ithaburensis*) can change their porosity under opposite environmental conditions (Lipshitz 1995). Thus, under stress conditions when extension growth is suppressed both tree species produced narrow annual rings characterized by ring-porous wood (as predicted by the limited-growth hypothesis), whereas under favorable conditions when extensive growth is intensive, both species produce wide annual rings with diffuse-porous wood (Lipshitz 1995).

The increased cambium sensitivity to IAA in ring-porous trees enables early cambium reactivation at the beginning of the growth season before bud break. This was evident in stem diameter measurements of the ring-porous *Zelkova serrata* saplings in their early leafless state, showing stem swelling 2–6 weeks before bud opening. During this developmental stage, actively dividing cambial cells, and immature slowly widening early-wood vessels that derived from them, are very soft, as they have not yet deposited their hard-secondary cell walls (Yoda et al. 2003), which therefore enables and promotes vessel widening.

The substantial increase in cambial sensitivity to auxin in ring-porous trees created the special internal conditions that enable them to respond to initial flows of extremely low-IAA concentrations originating in dormant looking (before swelling) buds a few weeks before bud break (Aloni 1991, 2001; Aloni and Peterson 1997; Aloni et al. 1997), stimulating slow vessel differentiation, which permits more time for cell expansion, promoting the widening of the differentiating earlywood vessels before their secondary wall deposition (as expected by the auxin gradient hypothesis of Aloni and Zimmermann 1983), resulting in the formation of very wide earlywood vessels. Therefore, the first wide earlywood vessels of ring-porous trees are initiated six to two weeks before the onset of leaf expansion (Suzuki et al. 1996; Sass-Klaassen et al. 2011; Takahashi et al. 2013; Lavrič et al. 2017; Puchalka et al. 2017; Gričar et al. 2020) and cause stem swelling before bud opening (Yoda et al. 2003). The pattern of earlywood vessel maturation in the ring-porous hardwoods, *Quercus serrata* and *Robinia pseudoacacia* progressed downward. The first mature earlywood vessel elements appeared at bud break, first at the top of the stem, and continue downward to the lower parts of the stem (Kudo et al. 2015).

Conversely, in diffuse-porous species, the first earlywood vessels are initiated two to seven weeks after the onset of leaf expansion (Suzuki et al. 1996; Takahashi et al. 2013), and because of the low cambium sensitivity in diffuse-porous trees, their cambium requires high auxin concentrations (from fast growing young leaves) for reactivation. These results explain the old report of Priestley and Scott (1936) who found that in a deciduous ring-porous tree the cambium undergoes extremely fast reactivation before bud break, which occurs almost simultaneously in the branches and along the trunk. This is why the bark of deciduous ring-porous trees may be peeled a few days before any bud swelling can be observed in spring. Conversely, a deciduous diffuse-porous species requires several weeks for a 'wave' of cambial reactivation to extend from the twigs of a large tree downward to the base of its trunk (Priestley and Scott 1936).

An opposite explanation for the differentiation of wide-earlywood-vessel in ring-porous trees was suggested by Wareing (1951) who studied cambial reactivation and wood formation in ring-porous versus diffuse-porous trees. Wareing suggested that the characteristic pattern of early rapid spread of cambium reactivation and the development of wide-earlywood vessels in ring-porous species "is due to the presence in the cambium of a reserve of auxin-precursor, which makes possible the rapid spread of wide-vessel formation throughout the tree, at an early stage of development of the buds". Wareing also mentioned the possibility that the dormant-looking buds of ring-porous trees that initiated cambial reactivation "were no longer 'physiologically' dormant" (Wareing 1951), in other words, it is possible that the dormant-looking buds possibly started to produce the auxin hormone.

On the contrary, experimental results on ring-porous trees (Aloni 1991) that aimed to test the limited growth hypothesis, demonstrated that the wide earlywood vessels are induced by very low auxin stimulation. Evidently, an extremely low-auxin concentration (0.003% Naphthaleneacetic acid (NAA) in lanolin w/w) applied to disbudded shoots of *Melia azedarach* trees, induced wide earlywood vessels (Fig. 3b) in the deciduous ring-porous trees (Aloni 1991, 2001), but this low-auxin concentration was not strong enough to stimulate any earlywood vessel differentiation in deciduous diffuse-porous trees (Aloni 2001). This was true also with 0.01% NAA (in lanolin) that induced more medium-size earlywood vessels (Fig. 3c) but was not strong enough to induce earlywood vessels in diffuse-porous trees. On the other hand, a high-auxin concentration (1% NAA in lanolin) induced rapid differentiation of narrow earlywood vessel in the ring-porous trees, because of fast secondary wall deposition that prevented vessel widening, and therefore remained narrow vessels (Fig. 3d). The high-auxin concentration induced earlywood vessel differentiation in diffuse-porous trees (Aloni 2001). These results clearly demonstrate that the wide earlywood vessels of a ring-porous tree are

induced by extremely low-auxin stimulation before bud swelling. Whereas in diffuse-porous trees there is a need for high-auxin concentrations produced in fast growing young leaves for inducing their typical regular size earlywood vessels (Aloni 1991, 2001, 2013a, 2021).

Fig. 3 The effect of auxin (1-Naphthaleneacetic acid (NAA) in lanolin) concentration on the width of earlywood vessel differentiation is shown in transverse sections in stems of the ring-porous tree *Melia azedarach*. All photomicrographs were taken from the same experiment, run in Tel Aviv from February 15 to March 15, 1986, and are presented in the same orientation and magnification (Bars = 250 μ m). All the sections were taken 50 mm below the apical bud, which was left intact (a), or was replaced by a range of auxin concentrations: low, 0.003% NAA (b), medium, 0.01% NAA (c), or high, 0.1% NAA (d). The auxin was applied in the form of a lanolin paste, which was renewed every 3 days. The photomicrographs show a substantial decrease in the diameter of the earlywood vessels (white arrows) with increasing auxin concentration (b–d). The low auxin concentration induced wide vessels (b). The two higher concentrations induced many more xylem cells (along a radius) with narrower vessels (c, d). The highest auxin concentration tested (0.1% NAA) resulted in very narrow earlywood vessels (d). The borderline between the latewood of 1985 (left) and the new earlywood of 1986 (right) is marked with white triangles. The experiment was repeated three times (in 1984, 1985, and 1986) with 5–10 stems per treatment; yielding the same results (from Aloni 1991)

The auxin produced by the buds and young leaves induces early vessel differentiation first immediately below the buds. Complete early differentiation of the earlywood vessels occurs first in the upper stem region, and then progresses to the middle and lower regions during bud swelling in the ring-porous *Quercus serrata* seedlings (Kudo et al. 2018). During this downward earlywood vessel differentiation process, the developing buds and young shoot organs are supplied by the functional network of previous year's narrow latewood vessels, while the wide earlywood vessels of the current year differentiate and slowly mature (Kudo et al. 2018).

6.3. Development of Two Wood-Porosity Patterns Along the Same Ring-Porous Tree

As was clarified above by the limited-growth hypothesis (Aloni 1991), for inducing the wide earlywood vessels in ring-porous trees there is the unique requirement for very low-auxin stimulation, originating in dormant-looking buds, early in the growth season along the very sensitive cambium of temperate deciduous ring-porous trees. These special conditions in the trunk of a ring-porous tree allow the early slow and long widening process of earlywood vessels, resulting in wide earlywood vessels before the secondary lignified wall is deposited (Aloni 1991; Suzuki et al. 1996; Sass-Klaassen et al. 2011; Takahashi et al. 2013; Lavrič et al. 2017; Puchałka et al. 2017).

A different pattern of vessel differentiation occurs in the twigs. In the youngest twigs, the secondary wall deposition and lignification of the first-formed vessels, relative to the time of leaf appearance, is faster in the more sensitive ring-porous trees, starting about two weeks earlier than in the twigs of the diffuse-porous trees (Takahashi et al. 2013). In ring-porous trees, the first-formed vessels of the year deposited lignified secondary walls in the twigs around the time of leaf appearance, at the time that the wide earlywood vessels in the trunk continue the slow widening process up to the deposition of their lignified secondary wall, occurring at full leaf expansion (Takahashi et al. 2013). The rapid vessel differentiation and early secondary wall deposition in the twigs does not allow

vessel expansion, resulting in narrow vessels in a diffuse-porous pattern in twigs of both the ring- and diffuse-porous trees. Therefore, in the two types of wood porosity trees, the wood produced in the twigs and branches during their first year (when they are only a few weeks/months old) is characterized by a diffuse-porous wood pattern (Cochard and Tyree 1990; Lo Gullo et al. 1995; Takahashi et al. 2013; Rodriguez-Zaccaro et al. 2019).

It should be emphasized that this diffuse-porous wood pattern in the youngest twigs/branches of ring-porous trees is induced by high-auxin concentrations produced by their young leaves, and it is not due to the influence of “cambial age”, as suggested by Rodriguez-Zaccaro et al. (2019).

Therefore, there is no need for “older cambia” to produce the wide earlywood vessels typical to ring-porous wood pattern (Rodriguez-Zaccaro et al. 2019), but only the requirement for the unique endogenous conditions of sensitive cambium that responds to extremely low-auxin stimulation, from dormant-looking and swelling buds, during early spring, allowing the slow vessel widening process typically forming the wide-earlywood vessels along the stem of temperate deciduous ring-porous trees (Aloni 1991, 2001, 2013a, 2021).

6.4. Leaf Phenology, Earlywood- and Latewood Development in Temperate Deciduous Hardwood Trees

Climate changes influence leaf phenology and tree development, which shape their adaptation and evolution; influencing cambial sensitivity, wood differentiation and vessel patterns. Fossil records indicate that the ring-porous wood pattern has developed under various environmental stresses especially during the past 50 million years, when the global climates have been undergoing active changes (Evert and Eichhorn 2013). The evolution of ring-porous trees has adapted them to survive under shorter and limiting growth seasons.

Diffuse-porous species start the growth season a few weeks earlier than ring-porous trees and have a longer growth season which is characterized by continuous production of auxin-producing young leaves during a few months (Aloni et al. 1997). Conversely, the more specialized ring-porous trees that are well adapted to limiting environments are late-leafing trees (Lechowicz 1984).

Ring-porous trees produce young leaves for only a short period of a few weeks and later they have mainly mature leaves (Aloni et al. 1997; Aloni 2021). Because young diffuse-porous trees possess greater growth intensity they might produce more xylem per year than young ring-porous trees (Aloni et al. 1997). In diffuse-porous trees, the continuous development of new auxin-producing young leaves along the growth season stimulates continuous production of new narrow vessels along the entire growth season with relatively thin-wall fibers. Whereas in ring-porous trees, the dominating mature leaves, which produce gibberellin (Aloni 1979; Dayan et al. 2012), induce the development of numerous well-developed hard lignified fibers during most of the growth season, with only a few narrow vessels limited in their width by gibberellin. These diverse earlywood and latewood properties in ring-porous wood, namely, the soft wide earlywood vessels versus the numerous hard thick-wall latewood fibers affect lumber stability and can have major effects on wood and fiber utilization.

7. Conclusions

The environment controls plant development by shaping plant's growth, its rate of development and morphology, which regulate plant's physiology and anatomy. During the process of plants

adaptation to their environments, there are gradual and continuous changes in the internal regulating hormonal mechanisms that shape the differentiation and structure of the vascular tissues.

The produced-leaf signal is modified during leaf development. The young growing leaf produced auxin, while during development the maturing leaf becomes a major source of gibberellin. The specific leaf's hormonal signal determines the type of the induced vascular element: auxin from young leaves induces vessels, while gibberellin from mature leaves is the specific signal that induces fibers.

The hormonal signal concentration determines the rate of cell differentiation. While the latter determines the final size of the conduit. Slow vessel differentiation induced by low-auxin stimulation, enables a long period of vessel widening until secondary wall deposition, resulting in the formation of wide vessels; e.g., either (1) at the base of stems of long lianas and tall trees away from the auxin-producing young leaves, or (2) at the earlywood of ring-porous trees characterized by sensitive cambium, where the earlywood vessels along the trunk are induced by extremely low-auxin-concentration streams, originating in dormant looking buds.

During the evolution of ring-porous trees under selective pressures of limiting environments, their natural stress selection has shortened the growth season, decreased vegetative growth and reduced foliar biomass, resulting in the reduction of the auxin hormone produced in young leaves. The latter promoted an increase in cytokinin levels inducing an increase in the sensitivity of the cambium to extremely low-concentration-auxin streams originating in dormant looking buds, before swelling, a few weeks before bud break. These low-auxin streams induce a slow and a long vessel widening process, which permits more cell expansion before secondary wall deposition, therefore resulting in the typical wide earlywood vessels of ring-porous trees.

Contrariwise, rapid vessel differentiation induced by high-auxin stimulation produced in young growing leaves results in narrow vessels in the new twigs and branches during their first growth season in both diffuse- and ring-porous trees; as well as in short trees, or along the upper parts of tall trees.

Although the late-leafing ring-porous trees have a shorter growth season, they have been well adapted to their limiting environment by producing wide and efficient earlywood vessels and numerous hard latewood fibers; the latter are induced by gibberellin produced in mature leaves. This combination makes the ring-porous trees very efficient in water uptake with very strong trunks due to their extremely wide earlywood vessels combined with thick lignified latewood fibers.

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The Figures

Fig. 1



Fig. 2

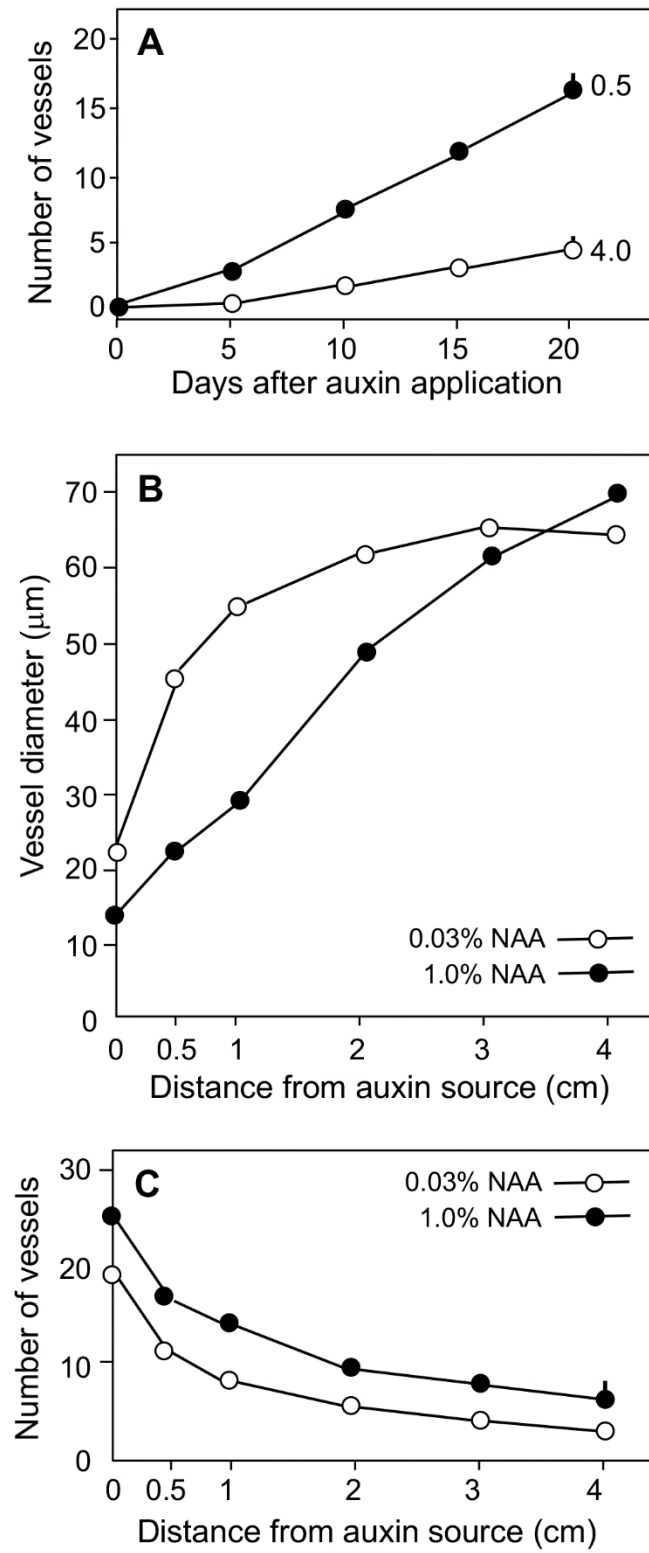


Fig. 3

