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Wulfenia **19** (2012): 57–95

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Functioning wood[1]

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Summary: Wood structure has been comprehensively examined in context of its functioning. Wood is considered to be a unit which performs simultaneously water-conducting and strengthening functions, though each of them requires contrastive characters of wood. Structure and patterns of tracheids/vessels of various woods conducting water longitudinally without decreasing the strength of the whole wood are presented. The lateral transport of water is shown to be of different importance in diffuse-porous and ring-porous woods. The diversity of formations maintaining such a transport is described compendiously. Conducting and strengthening functions of the axial parenchyma and rays are treated especially. Divergent evolution of conducting and strengthening subsystems of wood and their relative patterns are connected with evolutionary advancing of the paratracheal axial parenchyma. The advancement of the latter is shown to be an integral indicator of the advancement of heteroxylar wood.

Keywords: secondary wood, homoxylar, heteroxylar, manoxylic, pycnoxylic, tracheid, vessel, fiber tracheid, libriform fiber, axial parenchyma, ray, water conducting, wood strength, xylem evolution

Wood consists of diverse histological constituents. They compose a set of operational systems in accordance with their specific function/s. Conjunctions between the constituents of a system cause its functional integrity. Such systems combined structurally and functionally constitute wood as a whole. There are combinations between wood constituents and operational systems that allow the wood to perform its typical functions. Therefore, wood should be considered as an indissoluble unit instead of a conglomerate of different cells each functioning separately (Vikhrov 1954). That is why the very nature of the wood, i.e. its specific structure and physiology, can be seen only in the framework of 'functional xylotomy'. Concerning wood structure, a lot of data have been collected by now. Nevertheless, some essential traits of the wood still remain physiologically uninterpreted. They have been consequently neglected by xylotomists so far, though these traits are of great importance for the understanding of diversity and evolution of the xylem.

Longitudinal water conductance

It is well known that water is conducted through the wood by tracheids and vessels. The former are closed constructions of cell walls with bordered pits. The latter consist of numerous vessel segments. All segments except of the ultimate two have bordered pits in their longitudinal (lateral) walls and one to several perforations in both intervening transverse walls. Ultimate vessel segments have only one perforated wall, viz. the one adjacent to the penultimate segment, while all its other walls invariably bear bordered pits. Both tracheids and vessels are thus closed tubes. Therefore, the longitudinally conducted water has to percolate unavoidably from one closed tube to the next one through bordered pits in the tubes' walls. Thus, these pits are the key formations

1) Excerpted from miscellaneous articles of Gorn B. Kedrov (Appendix 1, 2) by A. C. Timonin.

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for intercommunicating water-conducting constituents of the wood. It is of great importance for realizing wood as a structural-functional unit, to investigate patterns of the bordered pits in the walls of tracheids and vessel segments, respectively.

Ratio between the pit number in tracheids' radial and tangential walls has usually been omitted in publications on wood anatomy. Very many xylotomists are used to scrutinizing pits *per se* (their shape, fine structure, relative position etc.) but to ignoring their locations in either radial or tangential walls of the tracheids. Accompanying illustrations often do not fill the gap of these data. However, the pattern of the pit location in tracheids' walls seems to be highly regular and constant in a taxon.

Vertical tracheids of secondary homoxylic (= vesselless) woods (SVWs) have repeatedly been shown to bear bordered pits mostly/exclusively in their radial walls in the vast majority of taxa having secondary homoxylic wood. Mostly/exclusively radial pitted walls of tracheids are inherent in all pycnoxylic cordaitaleans, extinct and extant ginkgoaleans, conifers and homoxylic dicotyledons (Jeffrey 1917; Scott 1923; Bailey & Swamy 1948; Metcalfe & Chalk 1950; Swamy & Bailey 1950; Yatsenko-Khmelevskiy 1954a,b; Hergert & Phinney 1954; Greguss 1955, 1967, 1972; Jane 1956; Takhtajan 1956; Vikhrov 1959; Budkevich 1961; Srivastava 1963; Yatsenko-Khmelevskiy & Shilkina 1964; Wagenführ 1966; Shilkina 1967; Lepekhina 1972; Maheshwari 1972; Patel 1974; Chavchavadze 1979; etc.) as well as in most manoxylic calamitaleans, sphenophylls, ferns, bennettitaleans, seed ferns and in nearly all cycads (Williamson & Scott 1894, 1895; Chamberlain 1911; Jeffrey 1917; Scott 1920, 1923; Greguss 1955, 1968; Takhtajan 1956; Süss & Müller-Stoll 1970; Rothwell 1975; etc.). A few manoxylic taxa have numerous pits equally distributed throughout radial and tangential walls of their tracheids. These are species of *Stangeria* and some species of *Zamia* of extant cycads and few members of extinct lepidodendroids (Williamson 1872; Jeffrey 1917; Scott 1920; Hirmer 1927; Henes 1959). I failed in searching plants with SVW whose tracheids have pits mostly/exclusively in their tangential walls. Such a pattern of pit location unlikely exists in vesselless secondary woods at all.

Pycnoxylic plants with secondary heteroxylic woods (SHW) contrast with their vesselless counterparts in patterns of pits in their tracheids. Pits are equally numerous in radial and tangential walls of tracheids in chlamydosperms (= gnetophytes) and many dicotyledons while in some dicotyledons, the pits in the tangential walls of tracheids outnumber those in the radial ones (Metcalfe & Chalk 1950; Shavrov 1956; Maheshwari & Vasil 1961).

Focussing on the relative positions of the tracheids in the SVWs, we now estimate the contribution of their pitted radial and tangential walls to the longitudinal conductivity of woods. The tracheids of the SVWs are well known to be in radial rows (Fig. 1 A). It's worth to stress that all tracheids of a row are nearly on the same level which can be seen in the radial section of the wood in Fig. 1 B. The tracheids of a row contact each other by their contiguous tangential walls, though the latter are often oblique tangential (Fig. 1 A). The terminal parts of rather many tracheids of a row have no tangential walls at all, because they are disconnected by intervening tracheids of one or both adjacent rows (Fig. 1 A, C: arrows). Instead of tangential walls, these parts have only oblique radial walls. Therefore, pits in the tracheids' tangential walls would be less numerous on average than those in the radial walls and also the average permeability of the tracheids' tangential walls would be less than that of the radial ones. Moreover, if all pits had been translocated from the radial

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walls of tracheids to their tangential walls, only lumens of the tracheids of the same radial row would have been in communication through such pits. In that case a radial water-conductance of the SVW would appear, but its longitudinal water-conductance would be completely lost because all tracheids of the row are on the same level. Additionally, the radial water-conductance would be discontinuous through the terminal parts of the tracheids due to the absence of the tangential walls there.

The tracheids of contiguous radial rows contact by their radial walls. The latter are flat and strictly radial if the tracheids stand opposite each other (Fig. 2 A), but they are usually be bent at obtuse angle if the tracheids alternate (Fig. 2 B). The angle between two flats of the same radial wall varies

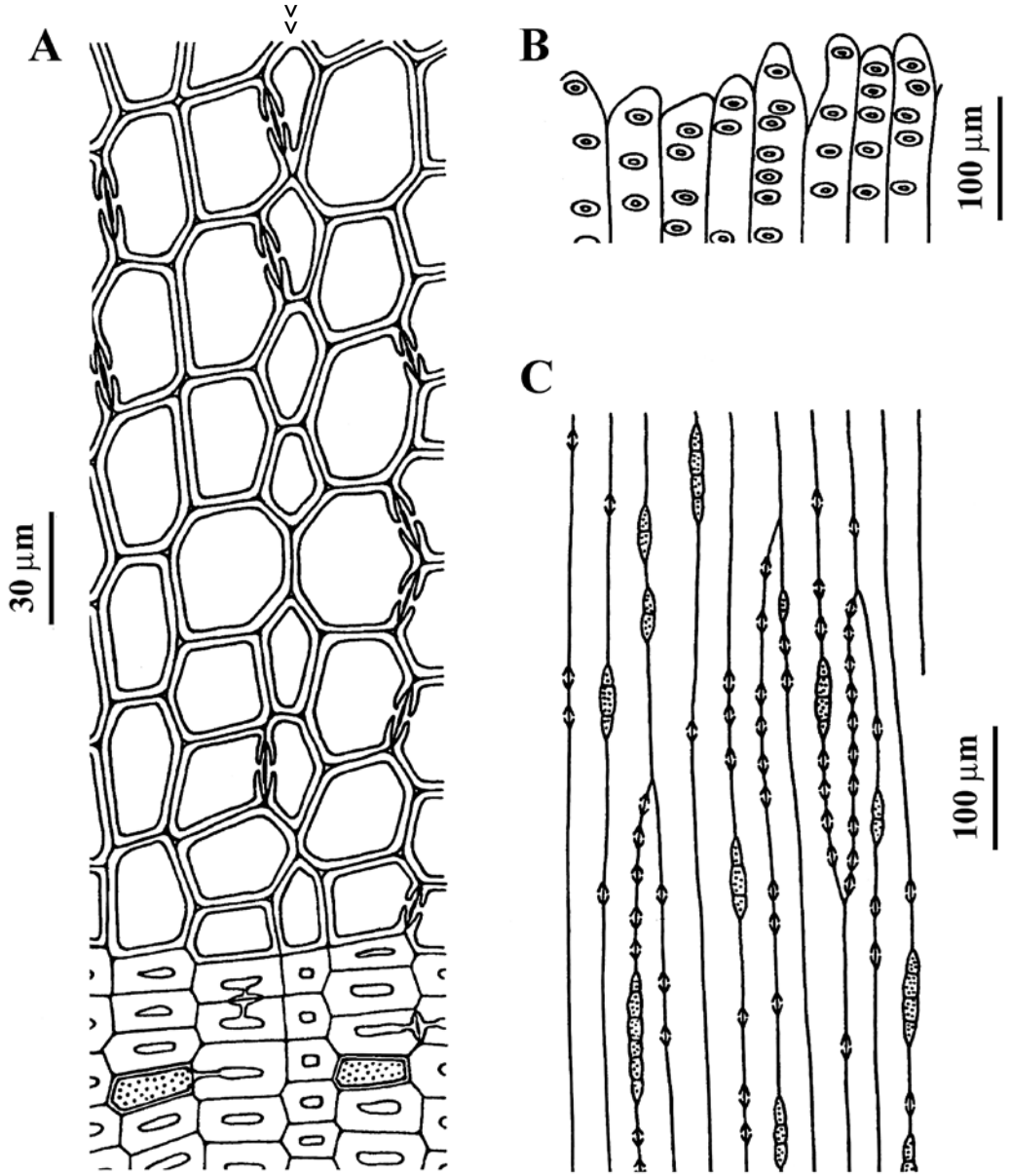

Figure 1. Arrangement of tracheids in SVW of *Cryptomeria japonica* D. Don. A – cross-sectioned wood; B – terminal parts of the tracheids in radial section of the wood; C – tangentially sectioned wood. *arrows* – radial row of the terminal parts of tracheids.

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from obtuse to right or even acute in few tracheids. Therein, the flats show nearly a front view in tangential sections of the wood. They thus simulate complete tangential walls of tracheids. Resultant misconceptions can be avoided by scrutinizing serial transversal sections of wood.

A non-storied position of the tracheids of different radial rows is inherent in every SVW. Thereof, the tracheids of contiguous rows variously overlap (Fig. 1 C). The bordered pits in radial walls of overlapping parts of tracheids of adjacent rows make the longitudinal water-conductance of the wood possible (Fig. 3). I compared specific lengths of these overlapping parts of the tracheids with the numbers of their shared pit pairs in *Larix dahurica* Turcz. and *Picea abies* (L.) Karst. The two characters greatly vary in both investigated species. On average 26.5, 22.1 and 3.0 shared pit pairs have been calculated in three samples of larch wood. Their tracheids overlap at 29.2%, 60.9% and 79.2% of their length. On average 37.8, 25.3 and 2.1 shared pit pairs have been revealed in three samples of spruce wood. Their tracheids overlap at 31.4%, 61.1% and 83.8% of their length. Therefore, the longer the overlapping parts of tracheids of contiguous radial rows are, the less numerous pits they bear. Storied tracheids were very rarely discovered in adjacent radial rows in wood samples of these species. Such tracheids contact each other nearly throughout. Their contiguous radial walls usually have no pits or only extremely few ones. Their lumens are thus completely isolated from each other or almost at least. Therein, the SVW of *Tetracentron sinensis* Oliv. is quite similar.

If non-storied tracheids of the SVW had changed to storied ones, the tracheids of the successive levels would have been connected by tiny terminal walls which would have borne very few bordered pits if any (Fig. 3 A: brackets). Only these few pits would function for longitudinal water-conducting. All other pits in the tracheids' radial walls would be futile for longitudinal water-conductance, because they enable water penetration only into the same-leveled tracheid/s of adjacent radial rows. Therefore, the SVW would be quite permeable to water tangentially but highly waterproof longitudinally.

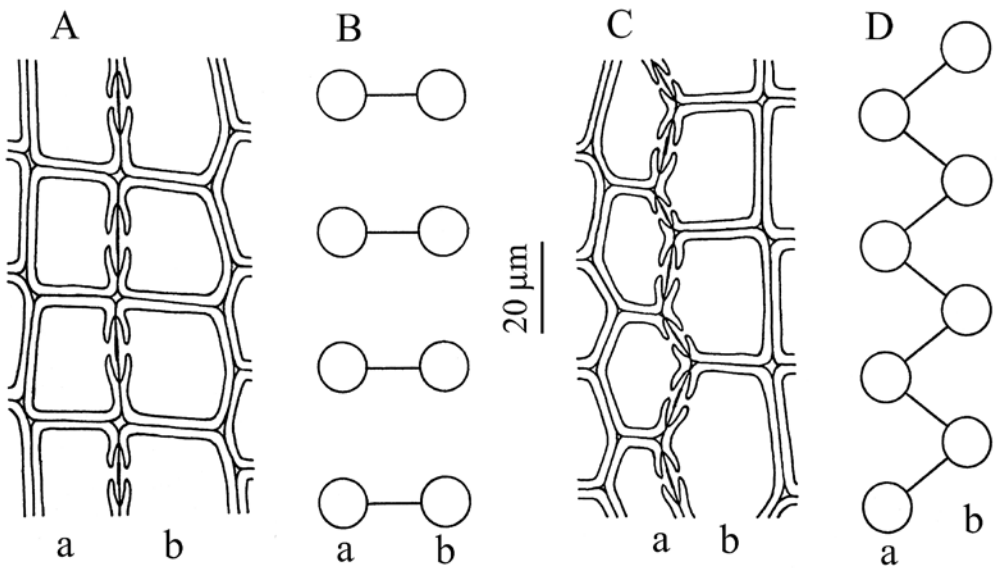

Figure 2. Communications between tracheids of adjacent radial rows in the SVW of *Thuja occidentalis* L. A, B – strictly tangential communications; C, D – oblique tangential communications. A, C – cross-sectioned rows of tracheids; B, D – diagrammed communications. *a, b* – tracheid rows.

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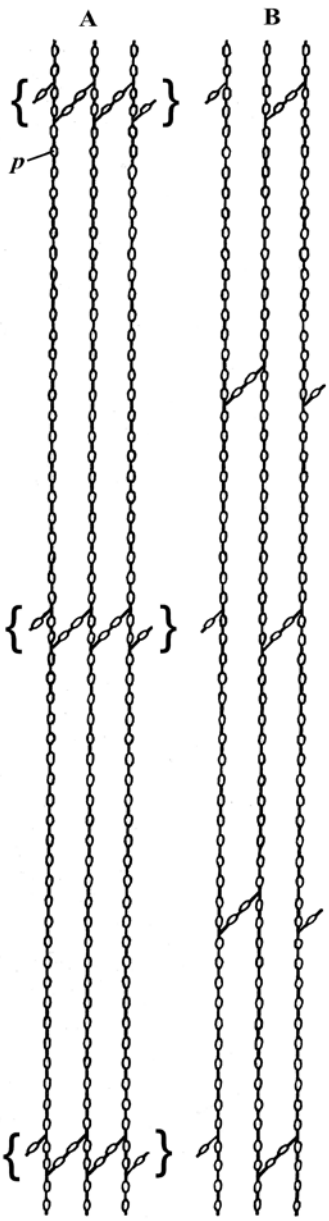
Both theoretically constructions, viz. exclusively tangentially pitted walls of storied tracheids would hardly allow the SVW to conduct water longitudinally. In real SVWs, water is longitudinally conducted only through the pits in the tracheids' radial walls. A non-storied pattern of the tracheids of different radial rows is *a sine qua non* character of SVW, because only this tracheid pattern results in a sufficient contact area for water-penetrating from one tracheid to the upward next (Fig. 3 B).

Vessels are the principal water-conducting constituents of the woods in the vast majority of dicotyledons. Every vessel is a closed capillary, because it has imperforated terminals on both of its ends. The vessels are always shorter than the length of the whole water-conducting tract of a plant. A set of vessels must inevitably intercommunicate to maintain longitudinal water current through the secondary heteroxylic woods (SHWs).



The SHWs markedly differ in communications between vessels. Tracheidal, direct and mixed (tracheidal + direct) communications, respectively, have been recognized in investigated woods.

There are many species whose vessels do not contact each other. For instance, *Cotoneaster integerrima* Med. has disjoint vessels and a lot of tracheids in between. The latter bear numerous large bordered pits to communicate with each other and with the vessel segments (Fig. 4 A). Vessel-to-vessel communications are evidently tracheidal in this species. In *Quercus robur* L., very many vessels adjoin at various lengths. However, the contact walls of the vessel segments are as thin as their other walls. Moreover, the contact walls have extremely few pits if any. Such vessels may be named 'contiguous vessels'. The contiguous vessels of the oak wood are embedded in a mass of tracheids with numerous conspicuous bordered pits in all their walls. These abundant tracheids really connect the vessels (Fig. 4 B). Similar tracheidal vessel-to-vessel communications are also inherent in *Buxus sempervirens* L., *Erica tetralix* L., *Crataegus oxyacantha* L., *Sorbus aucuparia* L., *Parottia persica* C. A. Mey., *Castanea* sp., *Rhamnus cathartica* L., *Pyrus* sp., among many others.

Fraxinus excelsior L. has no tracheids at all in its SHW. Its water-conducting system consists of only vessels which usually directly contact each other by the tangential walls of their segments. The vessels intercommunicate by means of very numerous bordered pits which occupy the whole contact area of their segments (Fig. 4 C). The contiguous walls of a vessel pair are flattened. Thereby, they have extended areas with increased pit numbers

Figure 3. Relative positions of the tracheids of contiguous radial rows in a SVW, tangential projection. A – theoretical positions; B – real positions. *p* – bordered pit; *braces* – contact areas of successive tracheids; see text for other explanations.

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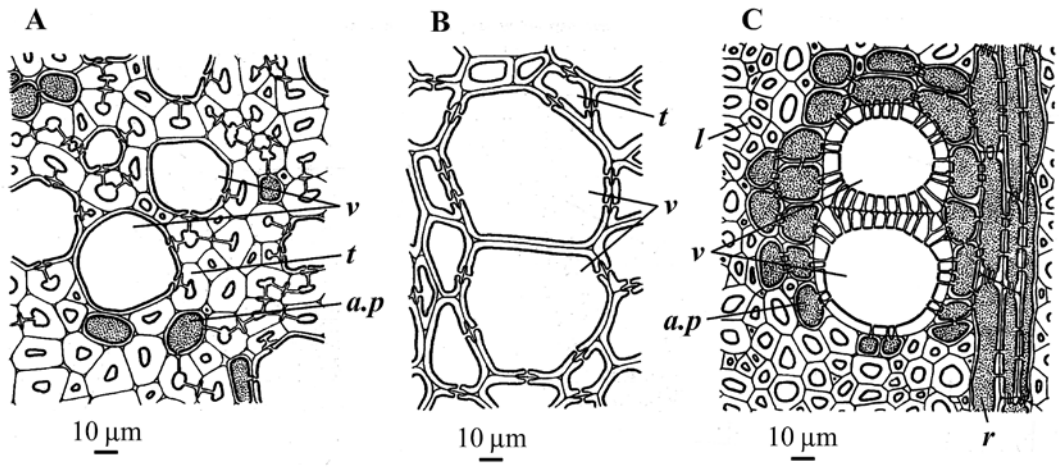
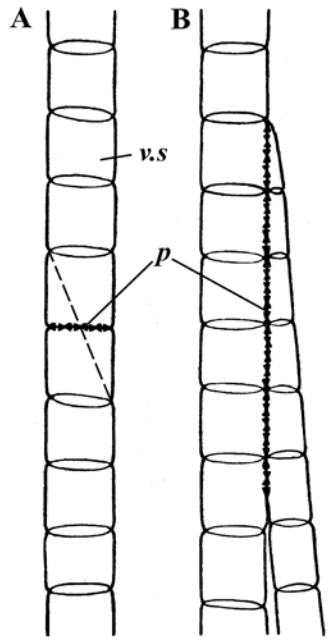


Figure 4. Cross-sectioned SHWs. A – *Cotoneaster integerrima* Medic.; B – *Quercus robur* L.; C – *Fraxinus excelsior* L. *a.p* – axial parenchyma; *l* – libriform fiber; *r* – ray; *t* – tracheid; *v* – vessel.

to enhance water-penetrating. The contiguous walls are clearly thicker than others of the vessel segment, perhaps, because of the fact that the water penetrates the pits under pressure. I name such vessels '*contact vessels*'. Only contact vessels are water-conducting constituents of the SHW of Braun's functional type V (Braun 1963).

Ivanov (1939) and Raskatov (1958) believed that water penetrated from one vessel to the next only through the bordered pits of the vessel's ultimate segments (Fig. 5 A). If so, the water-permeable area would be too small (about the area of vessel diameter) and the whole vessel system would consequently be water-resistant. On the contrary, Esau (1953) thought that successive vessels of a wood were variously overlapped like tracheids (see above). Either of the overlapping parts of the vessels are constituted by several end segments (Fig. 5 B). I analysed vessels of the ash wood and revealed that every vessel has rather numerous end segments which tangentially adjoin some middle parts of other vessel/s with a lot of its/their segments (Fig. 6). Such a vessel contact has been termed '*terminal communication*'. There is a large pitted vessel-to-vessel interface for efficient water-penetrating because the vessels consist of many vessel segments (Fig. 5 B). The terminal communications additionally enable the vessel to vary in number along the stem or root. My preliminary data on two branches of ash show that they have more spring wood vessels per growth ring just above the branching point than the trunk has below.



Vessels of ash wood also have *side communications* which can be seen in Fig. 7. Such communications occupy some middle parts of adjacent vessels and consist of one to few dozens of contiguous vessel segments. The segments of separate parts of vessels have evenly thickened walls throughout (Fig. 7 A). The vessel segments

Figure 5. Vessel-to-vessel communications. A – imaginary communication; B – real communication. *p* – pit; *v.s* – vessel segment.

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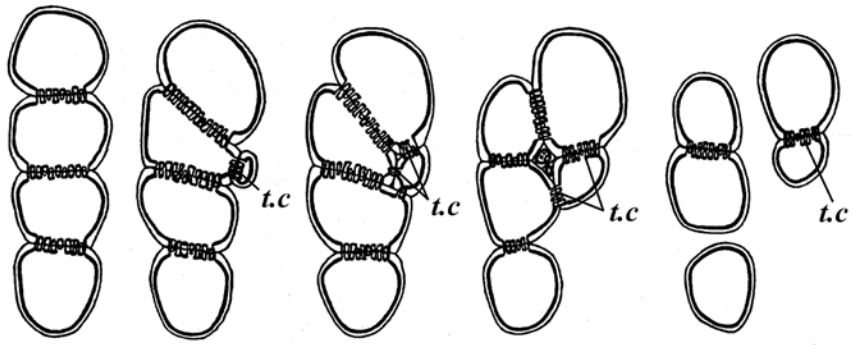

Figure 6. Terminal vessel-to-vessel communications in serial cross-sections of the root wood of *Fraxinus excelsior* L. *t.c* – terminal communication.

of the communicating parts of vessels have much thicker contiguous walls penetrated by typical bordered pits (Fig. 7 B–E). The wider the contiguous walls of the vessel segments are, the more bordered pits they bear (Fig. 7 B–C). The contacting vessels often, but not always, intertwine each other along their communication zone. Their intertwining usually takes about 180°, but it sometimes takes only 90° through ca. half length of the communication zone (Fig. 7 C–D) and turns back further on.

The number of the terminal communications of the vessels depends on the vessel lengths. The shorter the vessels are, the more numerous the vessel terminal communications per a length unit of the wood mass are, and the more water-resistant the wood is. However, shorter vessels have more side communications. The latter are always more numerous than their terminal counterparts in the trunk wood as well as in the root wood (Fig. 16). Therefore, they have totally a larger water-permeable area than the terminal communications. Consequently, the side communications highly enlarge the total water-permeable area of the wood to reduce essentially the resistance of the water-conducting system. The side communications of the vessels maintain the principal water current through the wood. The terminal communications are of minor importance for conducting water.

Combined tracheidal and direct vessel-to-vessel communications are inherent in woods with vessels and tracheids. However, significance of each communication type varies in different plants.

There are very few direct vessel-to-vessel communications in the SHW of *Cornus alba* L. Contact zones of the vessels have only few scanty pits. On the contrary, copious tracheids have numerous large pits per cell (Fig. 8 A). Thereof, the tracheids are the principal passages between vessels, while immediate vessel contacts are insignificant. A similar structure of the water-conducting

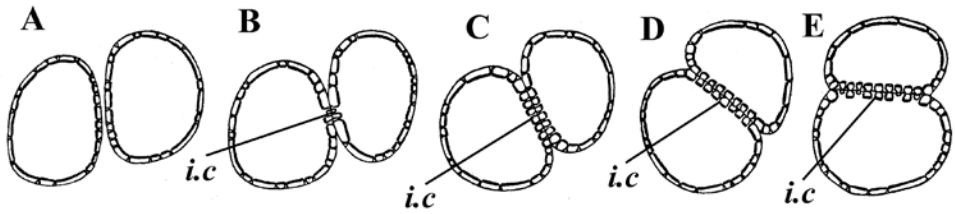

Figure 7. Side vessel-to-vessel communications in serial cross-sections of the trunk wood of *Fraxinus excelsior* L. *i.c* – side communication.

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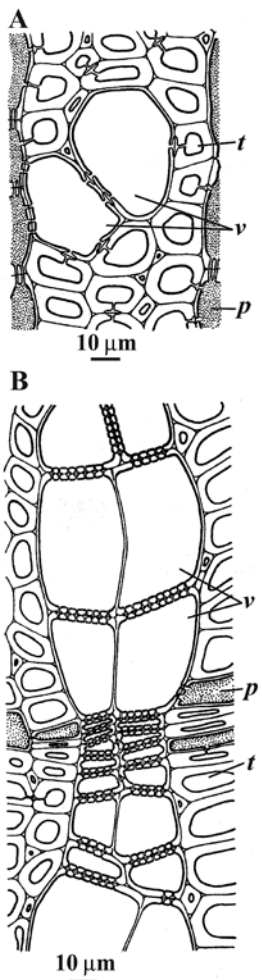
system was revealed in SHWs of *Fagus sylvatica* L., *Ostrya carpinifolia* Scop., *Malus praecox* (Pall.) Borkh., *Lonicera caerulea* L., among many others.

Betula pendula Roth shows mostly direct vessel-to-vessel communication in its wood, though the tracheids do slightly contribute to vessel intercommunications. Accordingly, there are very many vessel-contact zones with copious densely packed pits in birch wood. The tracheids are also numerous, but each has few tiny pits (Fig. 8 B). Additionally, this type of vessel communication is inherent in *Liriodendron tulipifera* L., *Prunus padus* L., *Salix alba* L., *Sambucus racemosa* L., *Corylus avellana* L. etc.

Vessel-to-vessel communication types strictly correlate with the histological composition of the wood. There are always tracheids with conspicuous pits in wood with tracheidal type of vessel-to-vessel communications. There are certainly advanced direct vessel-to-vessel communications in woods without tracheids. However, presence of tracheids in wood does not exclude direct vessel-to-vessel communications in it and *vice versa*.

Plant physiologists have shown that the water-conducting system of wood enables solved organic and inorganic substances to be transferred from the roots to the leaves by transpiratorily ascending xylem sap (Clarkson 1974; Kramer & Kozlowski 1960, 1979; Kursanov 1976; Lyr et al. 1967; Moorby 1981; Zimmermann & Brown 1974). The descending current of water beeing absorbed by leaves has also been revealed in some plants (Kramer & Kozlowski 1960, 1979; Lyr et al. 1967; Slayter 1956, 1967). Slayter (1956, 1967) believes that both ascending and descending water currents are kept by the same constituents of the plant body. It is still unclear, if organic and inorganic substances being in leaves as well as extraroot fertilizers absorbed by the latter are taken away from the leaves by descending xylem sap (Vaganov 1953; Libbert 1974) or only by the phloem sap (Clarkson 1974; Kramer & Kozlowski 1960, 1979; Lyr et al. 1974; Haynes & Goh 1977).



Young oak trees, 45–60 cm tall with circularly debarked trunks, were used to solve this uncertainty. The trees were kept under water stress for 10 days. Thereafter, $K_2H^{32}PO_4$ combined with detergent Tween 20 was put on their leaves for 90 sec. Radioactive ^{32}P was detected in the trunks below their debarked parts soon afterwards. Thus, $K_2H^{32}PO_4$ was conducted downwards the trunk in a short period of time. Only the wood could evidently have conducted this substance, because the descending phloem conductance was completely blocked by debarking. The descending flow of $K_2H^{32}PO_4$ through the oak trunks seemed to be powered by resilience of the walls of water-conducting constituents of the wood (see Kedrov 1985 for more details).

Nobel (1970) formulated the *cohesion theory*: water molecules in tracheary elements are cohesively fastened together and are also firmly

Figure 8. Cross-sectioned SHWs. A – *Cornus alba* L.; B – *Betula pendula* Roth. *p* – parenchyma; *t* – tracheid; *v* – vessel.

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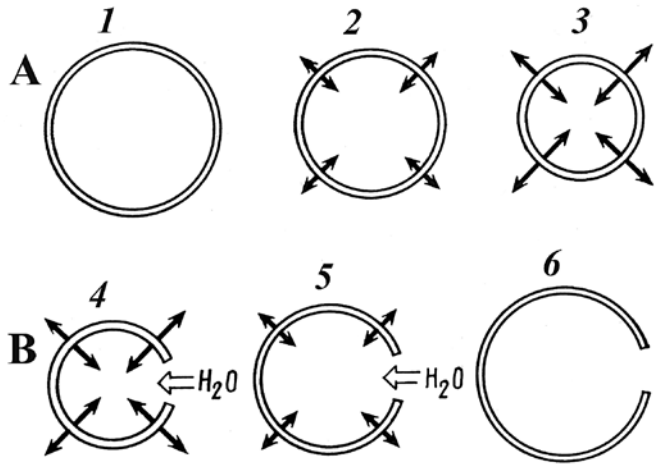

Figure 9. Diagram of forces affecting tracheary element wall. A – deforming forces and their counter-forces that appear in the walls of desiccating tracheary element; B – forces that cause water-sucking into injured tracheary element. 1–3 – contracting tracheary element under water stress; 4–6 – restoring tracheary element which sucks water through injury.

adhered to the element's walls. The water stress causes hydrostatic tension in these elements, but both cohesion and adhesion of the water molecules prevent the water filament therein from rupturing. The hydrostatic tension can rise up to several dozens or even hundreds atmospheres (Scholander et al. 1965). Combined cohesion and adhesion of the water molecules pull on the walls of the tracheary elements inwards to cause contraction of the latter (Fig. 9 A). This contraction simultaneously generates centrifugal counter-forces in the walls of the tracheary elements. Elastic deformity of the tracheary elements as well as the whole wood resultantly appear (Fig. 9 A). The water-conducting system becomes thereof able to suck water in through any injury. The water being sucked causes a decreasing of the hydrostatic tension in the tracheary elements. Accordingly, the contracting forces in the walls of the latter are also decreasing. As a result the tracheary elements are restoring their shapes due to the resistance of their walls (Fig. 9 B). The water thus sucked and all its solutes can be conducted rapidly, distantly and bidirectionally by the plant's tracheary elements. It can be conducted even downwards from the leaves to the roots (Hatch & Glasziou 1964; Nelson & Gorham 1957, 1959). Volume of the sucked solution, velocity of solution current and distance seem to depend on water deficiency in plant body.

The same mechanism of the descending current containing ^{32}P certainly took place in the experiment with oak, though the radioactive phosphorus was put onto intact leaves. Water deficiency usually arises in the leaf mesophyll cells. Therefrom, it passes through the leaf veins to the branches and then to the trunk to reach the roots (Kramer & Kozlowski 1960; Lyr et al. 1967). That is why the xylem terminals of the leaf veins must be the initial sites of the descending ^{32}P current in the wood of the investigated oaks rather than the phloem above the debarked parts of the trunks. The substance under consideration is likely to have penetrated the veins from the apoplast *via* their parenchymal sheaths. Perhaps, leaf substances can similarly be carried out of the leaves by the descending flow of water which has been absorbed by intact leaves from rainfalls and dews.

The descending solute currents through the water-conducting systems are only possible in the case of water deficiency. This current is similar to the solute current through the phloem in

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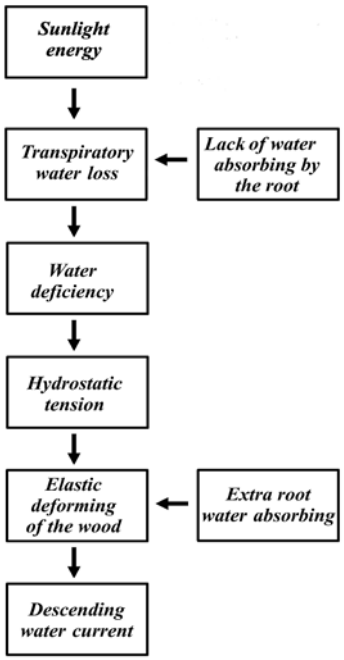

Figure 10. Diagram of consecutive processes resulting in a descending water current through the wood.

its direction, but it does not need any resources of the plant. Indeed, the descending solute current through the wood is generated by sunlight energy which has been transformed into potential energy of elastically deformed walls of the wood constituents by means of transpiration (Fig. 10).

Radial water conductance

The longitudinally ascending water current is combined with radial one in the secondary woods of growing woody plants which is directed outwards. That's because the foliage of annual shoots is supplied by only one to a few outer growth rings of sapwood. Thereof, the water current must pass from the inner sapwood to the outer one to arrive in the foliage leaves. Then, the radial water conduction of the wood is as regular as the longitudinal one. Therefore, there are special formations in the secondary wood transmitting water currents outwards to the outer sapwood.

Most members of Pinaceae have ray tracheids which constitute continuous radial rows and conduct the water directly outwards (Ivanov 1939; Yatsenko-Khmelevskiy 1948, 1954b, 1961; Greguss 1955; Jane 1956; Takhtajan 1956; Budkevich 1961; Chavchavadze 1979). In *Tetracentron sinensis* Oliv. SVW the water is radially conducted by special short vertical tracheids (Thompson & Bailey 1916). These tracheids are in continuous radial rows and intercommunicate directly by means of numerous bordered pits in their contiguous tangential walls (Fig. 11). All other homoxylar woody plants don't have special formations for radial water conduction in their SVWs. However, Krassulin (1941) revealed that successive growth rings of the SVWs of firs effectively intercommunicate in spite of the absence of ray tracheids.

Ivanov (1939) and Vikhrov (1954) believed that parenchymal rays conducted most of the water outwards. However, the water current speed in living protoplasts is 0.01–0.03 mm/h under 1 atm. (Sabinin 1955; Raskatov 1958). The parenchyma conducts water at 1–6 cm/h or even slowlier (Clarkson 1974; Libbert 1974) whereas the upward transpiratory water current can reach a speed of several dozen mph in secondary woods (Huber 1935; Akhromeyko & Zhuravleva 1956; Greenidge 1958; Kramer & Kozlowski 1960; etc.). Longitudinal water

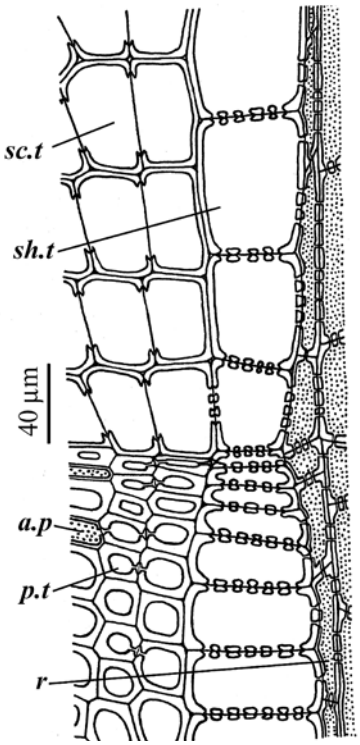

Figure 11. Cross-sectioned SVW of *Tetracentron sinensis* Oliv. *a.p* – axial parenchyma; *p.t* – pitted tracheid of the summer wood; *r* – ray; *sc.t* – scalariform tracheid of the spring wood; *sh.t* – short tracheid to conduct water radially.

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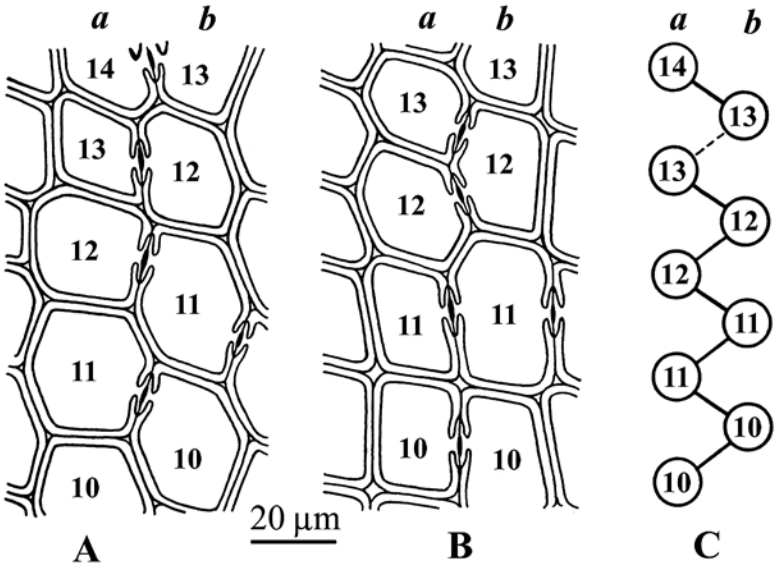

Figure 12. Radial communications between tracheids of the spring wood in *Thuja occidentalis* L. A, B – serially cross-sectioned wood; C – diagram of communications. *a, b* – contiguous rows of the tracheids; *arabics* – numbers of the successive tracheids in a row.

conductivity of non-tracheary wood elements does not exceed 1.85% vessel conductivity (Lugowoi 1914). Radial water conductivity of non-tracheary wood elements seems to be similar. Thereof, the non-tracheary elements of wood are insufficient to conduct the needed water radially.

My functional and anatomical investigations of the SVWs of *Thuja occidentalis* L., *Juniperus communis* L. and *Abies sibirica* Ledeb., which have no ray tracheids, show that the water is conducted outwards by the vertical tracheids there. Figure 12 shows two cross-sections of the same spring wood tracheids of *Thuja occidentalis* L. in a distance of 165 µm (level A and level B). None of the tracheids has pits in its tangential walls. Therefore, there are no direct radial communications between the tracheids. The tracheid 12b seen in Fig. 12 B communicates directly with the tracheids 12a and 13a of adjacent radial row of tracheids. The tracheids 12a and 13a intercommunicate thereby indirectly. Contiguities between tracheids of the rows 'a' and 'b' change lengthwise. The tracheid 11a communicates with the tracheid 10b on the cross-section level A (Fig. 12 A) while it communicates with the tracheid 11b on the ross section level B (Fig. 12 B). Then, the tracheids 10b and 11b intercommunicate *via* the tracheid 11a. The transverse plane projection of all direct communications between tracheids throughout their lengths shows that all tracheids of each radial row indirectly intercommunicate (Fig. 12 C) in spite of the absence of their pitted tangential walls. A set of these indirect intercommunications constitutes a continuous system of radial water conduction.

The above-mentioned change of tracheid contiguities takes place in roots, stems and branches of all investigated plants. It is caused by the curvature of the tracheids whose ends are always bent inwards (Fig. 13). Most bordered pits are in these ends. Such positions of the pits are evidently conducive to an indirect communication between tracheids of every radial row. These indirect communications between tracheids of the same row also take place in the summer woods of any growth ring. However, the summer wood tracheids sometimes have rather numerous bordered pits in their contiguous tangential walls to enable direct radial intercommunications. The summer

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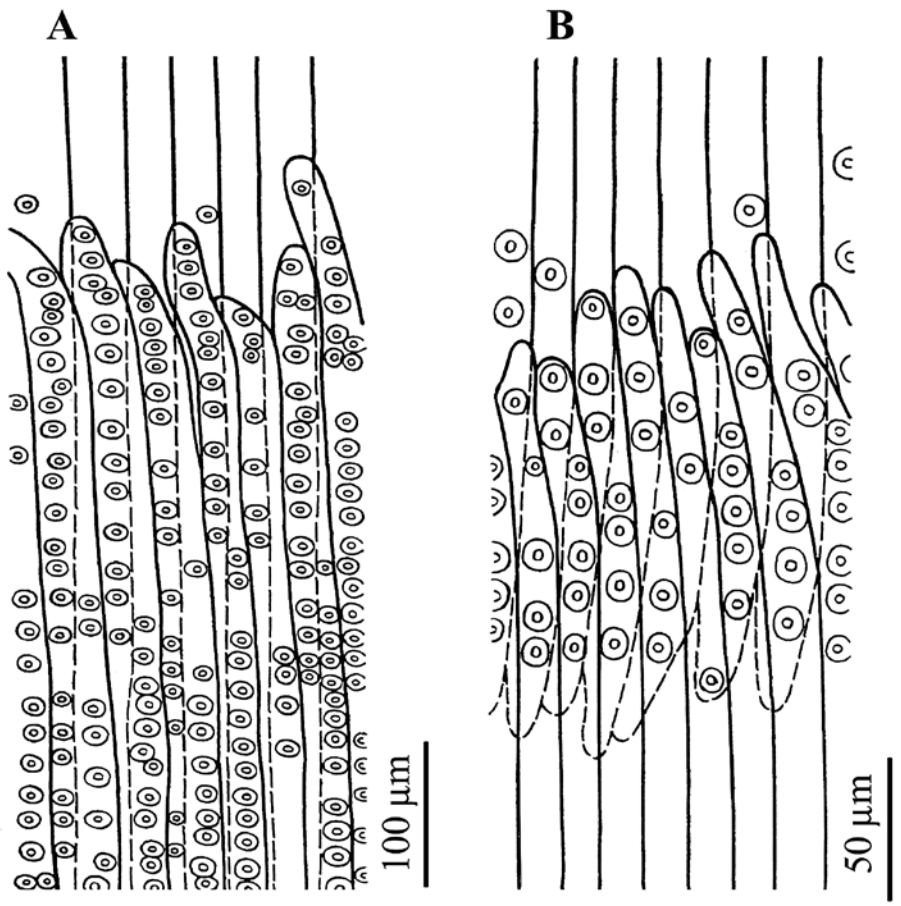

Figure 13. Radial sections of the SVWs, inward bending of the terminal parts of tracheids. A – root wood of *Thuja occidentalis* L.; B – trunk wood of *Juniperus communis* L.

wood tracheids of a growth ring mostly communicate with their spring wood counterparts of the next ring by means of bordered pits in their contiguous tangential walls (Fig. 14 A). Additionally, the end parts of the spring wood tracheids often grow intrusively into the mass of the summer wood tracheids of the preceding growth ring. Then, the (parts of) radial walls of the arising spring wood tracheids are contiguous with the (parts of) radial walls of their preceding summer wood counterparts. These contiguous (parts of) radial walls of spring wood and summer wood tracheids quite often bear bordered pits (Fig. 14 B). Thus, the bordered pits in tangential walls and those in radial ones cooperatively enable direct communications between the summer wood tracheids and the next spring wood tracheids. These bordered pits are on different levels in different tracheids. Thereof, radial water currents are not strictly radial (horizontal) but they undulate longitudinally and tangentially.

Every tracheid has bordered pits in its radial and tangential walls in SHWs with tracheidal and mixed vessel-to-vessel communications which are inherent in chlamydosperms and many woody dicotyledons; the bordered pits are even more numerous in tangential than in radial walls of tracheids in some dicotyledons (Metcalfe & Chalk 1950; Shavrov 1956; Maheshwari & Vasil 1961). Pits in tangential walls immediately pass on water in radial direction. The SHWs with only direct vessel-to-vessel communications have wavy vessels. Their sinuosity is mostly

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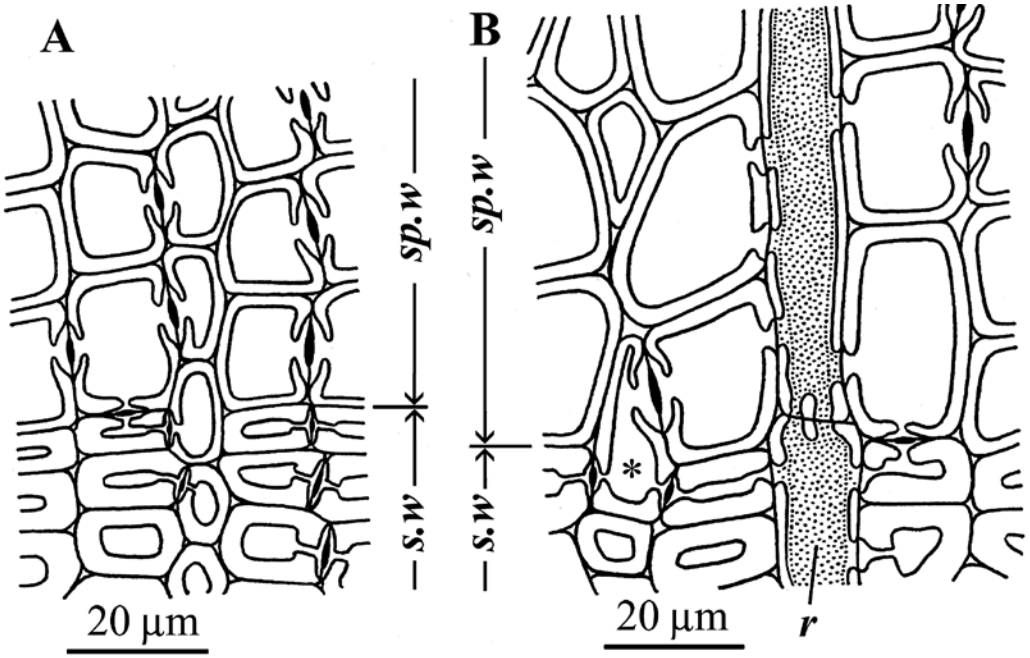

Figure 14. Cross-sectioned SVWs. A – branch wood of *Juniperus communis* L.; B – root wood of *Abies sibirica* Ledeb. *r* – ray; *s.w* – summer wood; *sp.w* – spring wood; *asterisk* – spring wood tracheid intruded into the mass of summer wood counterparts.

tangential but radial sinuosity also occurs (Fig. 15). Such vessels are united into a continuous 3D conducting system by means of mainly side vessel-to-vessel communications. This vessel system conducts the water in three principal directions, viz. upward longitudinally, tangentially and outward radially. However, there are no radial rows of such vessels that cross the whole growth ring of SHW. Therefore, there is no strictly radial conducting of the xylem sap in these woods (Fig. 16).

In ring-porous SHWs, the water is mostly conducted by the outermost growth ring, whereas in the diffuse-porous ones several peripheral growth rings take part in water-conduction (Raskatov 1958; Kozlowski & Winget 1963). Therefore, the more advanced system of radial water-conduction must be inherent in species with diffuse-porous woods.

The root wood of *Fraxinus excelsior* L. is diffuse-porous. Its spring wood vessels contact each other and also summer wood vessels of the same growth ring. The latter contact the spring wood vessels of the next outer growth ring (Fig. 16). Their total contact area along the root is large enough to make the boundaries between successive growth rings quite permeable for radial water current.

The trunk wood of *Fraxinus excelsior* L. is clearly ring-porous. Accordingly, there are extremely few contacts between spring wood and summer wood vessels of the same growth ring as well as between summer wood vessels of a growth ring and spring wood vessels of the next outer growth ring. Such contacts are only detectable if a very long piece of the stem/trunk is scrutinized. The distinctive system of radial water conduction in the diffuse-porous SHW of ash's roots thus decreases to nearly absent in the ring-porous SHW of its trunk. Nevertheless, all vessels of ash's wood are united in a 3D system, which conducts water longitudinally, radially and tangentially, by means of terminal and side communications.

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In sum, longitudinal water current in SHWs of ash's roots and stems runs from vessel to vessel mostly through side vessel-to-vessel communications but also through terminal ones. Thereof, the current deviates mostly tangentially to approach gradually at the outer boundary of the growth ring. At the boundary, the water current passes to the outer growth ring through trans-boundary vessel-to-vessel communications.

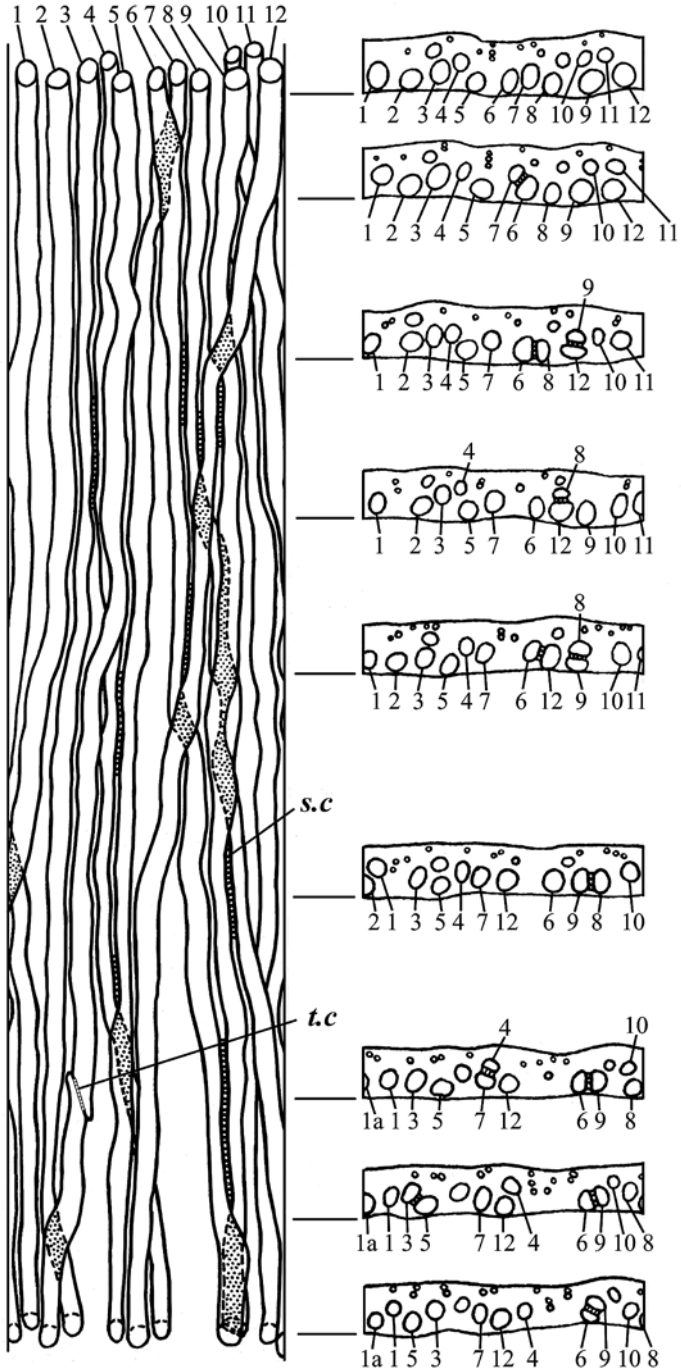

Figure 15. Arrangement of the spring wood vessels of a growth ring in a 2 cm long block of trunk SHW in *Fraxinus excelsior* L. *s.c* – side communications; *t.c* – terminal communication.

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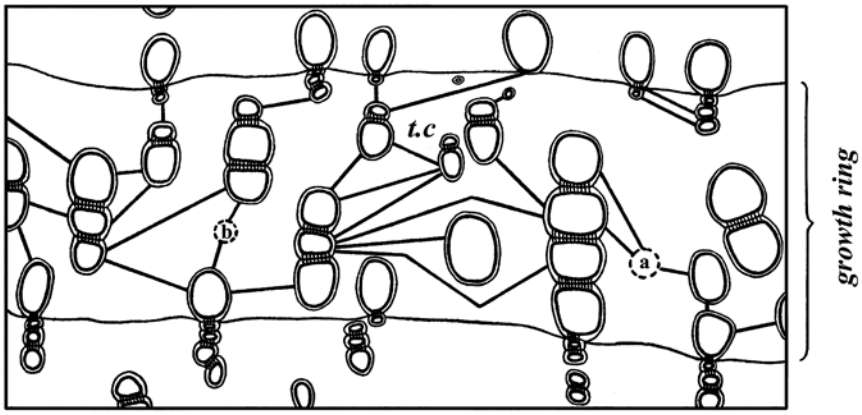

Figure 16. Diagram of communications between vessels in a 1 cm long block of root SHW in *Fraxinus excelsior* L. *a, b* – vessels that appear downward the block; *t.c* – terminal vessel-to-vessel communication.

Strength of wood

Seward (1917) introduced terms 'manoxylic' and 'pycnoxylic' to indicate the structure of SVWs of cycads and conifers, respectively. Yatsenko-Khmelevskiy & Shilkina (1964) reconsidered both terms to characterize the contribution of the secondary wood to stem stiffness compared to parenchyma, periderm etc. but not to characterize the structure of wood *per se*. The primary xylem and secondary wood (if present) are only subsidiary strenghtening constituents of manoxylic stems, because they only comprise a small specific volume of the stem. Stiffness of manoxylic stems is principally caused by mostly peripheral stem tissues outside the xylem. In the pycnoxylic stem, abundant secondary wood occupies most of its volume. Thereof, the stiffness of such a stem is nearly completely caused by its secondary wood.

Thus, the secondary wood of pycnoxylic stems combines conducting and strengthening functions. It consists of structurally and functionally uniform vertical constituents in a few extant conifers and woody dicotyledons, e.g. some species of *Araucaria*, *Dacrydium* and *Podocarpus* (Greguss 1955; Chavchavadze 1979) and some species of *Bubbia*, *Belliolum* and *Exospermum* of homoxylar dicotyledons (Carlquist 1982, 1983a, b). Each of them has a SVW. The more numerous the bordered pits in tracheid walls are, the less resistant the tracheids are against compressing and stretching forces. The same is true for the cohesion of tracheids. Decreasing of the pit numbers per tracheid must have been a mainstream in the evolutionary advancing of the examined woods. However, numerous bordered pits are necessary for conducting water, but their importance basically differs in accordance with their position in the tracheid walls. As shown above, the pits in tracheid tangential walls are absolutely ineffective in longitudinal and tangential water conduction. Concerning radial water conduction, these pits are easily substitutable by other formations of the xylem. Therefore, bordered pits in tangential walls of tracheids reduced during evolution to improve the strength of the concerned woods. As a result, they have nowadays only few bordered pits per cell, if any, in the tangential walls of their constituent tracheids.

The vast majority of conifers and woody dicotyledons have rather dissimilar conducting and strengthening constituents of their secondary woods, though both functions are often differently combined in a constituent. Two principal designs of such woods were recognized on the base of patterns of these two types of constituents.

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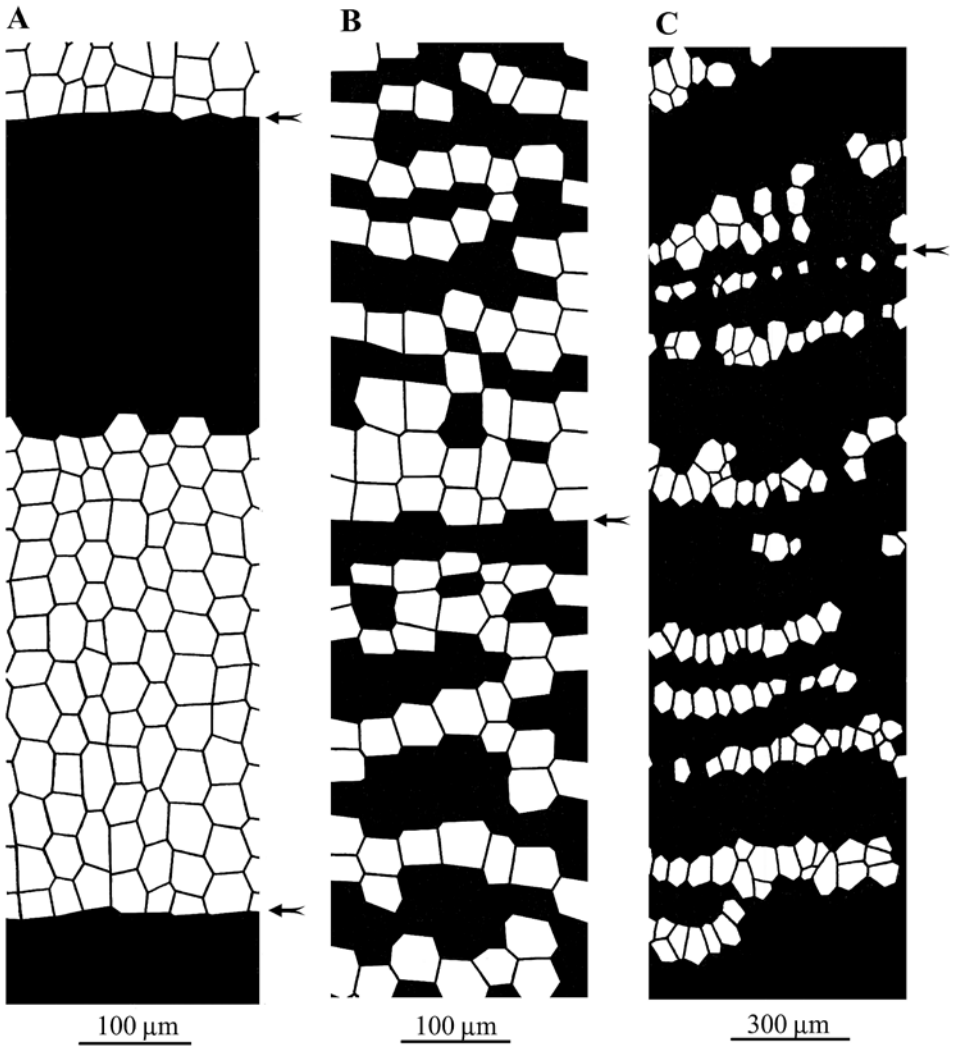

Figure 17. Patterns of water-conducting (white) and strengthening (black) constituents of the wood, cross-sections. A – *Larix dahurica* Turcz.; B – *Ginkgo biloba* L.; C – *Guevina avellana* Molina (Proteaceae). *arrows* – boundaries of growth rings.

The circular growth ring design shows spring wood mostly containing water-conducting tracheary elements and summer wood mostly containing strengthening ones (Fig. 17 A). The diffuse growth ring design is characterized by the rather evenly interposed wood constituents of both types through the growth ring, though the strengthening ones are usually in various discernible aggregates (Fig. 17 B). Some species have just one of these designs of their secondary woods, while others have both.

Only the circular growth ring design is inherent in most conifers and some vesselless dicotyledons as *Tetracentron*, *Trochodendron* (Metcalfe & Chalk 1950) and some species of *Pseudowintera* (Patel 1974). This design is more evident in plants inhabiting areas of distinctive seasonal climates. Their summer wood tracheids differently participate in water conduction.

In all investigated samples of arborvitae, all tracheids of a growth ring contained xylem sap. Each tracheid of this species thus combines water-conducting and strengthening functions. The same

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situation, viz. all tracheids filled with xylem sap, was discovered in some growth rings of samples of fir wood. However, gas was detected in several tracheids, which are located in 0.1 mm wide (or narrower) transitional zone between spring wood and summer wood in growth rings of fir. Such tracheids are certainly unable to conduct water. They consequently function as purely strengthening constituents of the SVW. Scanty (in fir) to absent (in arborvitae) gas-containing strengthening tracheids seem to be the result of the absence of ray tracheids in these two trees. Because there are no ray tracheids, the water is conducted radially by the ordinary vertical tracheids. If all summer wood tracheids or very many of them had contained gas, outward transport of the water from one growth ring to the next would have been impossible.

Perelygin (1954) discovered that every summer wood tracheid of pine and larch woods communicates with another one/s by means of bordered pits, although the larch is well known to have very few bordered pits in its summer wood tracheids. Nevertheless, gas was detected in all vertical tracheids of the summer woods of pine, larch and spruce as well as in those of hemlock and two more *Pinus* species (Harris 1961). On the contrary, gas was never detected in the tracheids of the transitional zone[2] between spring wood and summer wood of these conifers. Gas in the summer wood tracheids prevents them from conducting water longitudinally, but does not interrupt the radial water current to the next outer growth ring. The fact is that these conifers have ray tracheids in their woods which maintain direct radial water current, irrespective of the functioning of the summer wood vertical tracheids.

The diffuse growth ring design is inherent in the SHW in dicotyledons growing in areas with climates without seasons. Most of them have fiber tracheids as principal strengthening constituents of their woods. These tracheids also take part in the water conduction because they are intermediates between vessels (tracheidal vessel-to-vessel communications, see above). The strengthening system consists of only non-conducting libriform fibers in woods of Braun's (1963) most advanced functional type. The libriform fibers mostly contain gas, irrespective of their location in the growth ring (Braun 1963). But some woody dicotyledons have living libriform fibers, which contain protoplasts (Braun 1963) and are unable to let in air. (The living libriform fibers of maple constitute vessel sheaths.)

Combined circular and diffuse growth ring designs are characteristic of SHWs in dicotyledons growing in areas of seasonal climates.

The SVW of ginkgo strikingly differs from SVWs of conifers and other pycnoxylic gymnosperms in their two types of vertical tracheids, viz. the wide and narrow ones (Greguss 1955; Srivastava 1963). The latter are scattered throughout the growth ring in irregular groups. They have extremely few pits, if any, that connect them to each other or to the wide counterparts. The narrow tracheids bear bordered pits to communicate with ray cells. They do not grow intrusively during the period of their development from the cambial derivatives (Chattaway 1936; Carlquist 1975). Thereof, these formations cannot be attributed as the libriform fibers. The structure of investigated samples of SVW of ginkgo shows the following characteristics. The wide tracheids take about 45% of the total number of tracheids. They have thinner walls with numerous bordered pits to communicate with other tracheids and ray cells. Approximately 16% tracheids are narrow ones mostly communicating with ray cells by means of bordered pits, but they also

2) Transitional zones in the growth rings are quite evident in the spruce wood, but rather unclear in pine wood and indistinctive in larch wood.

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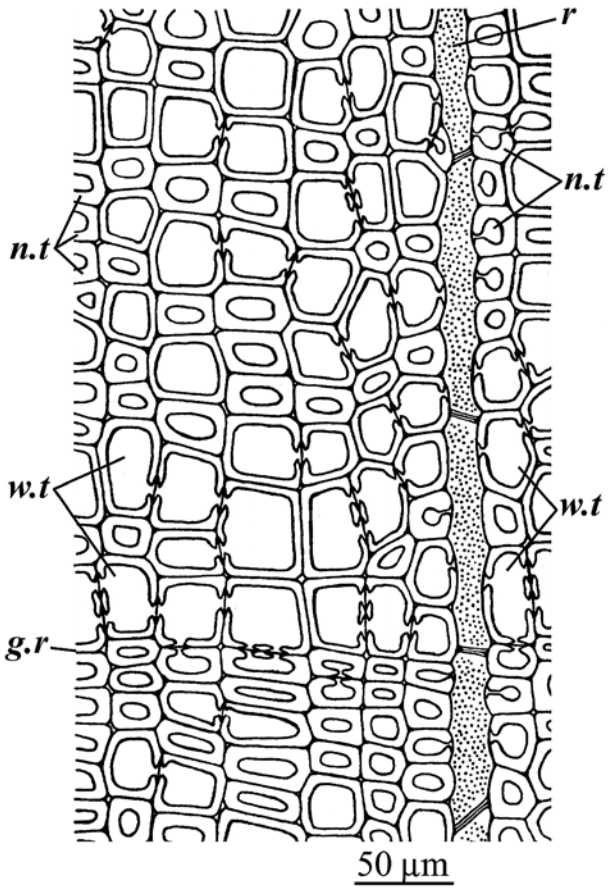

Figure 18. Cross-sectioned SVW of *Ginkgo biloba* L. *g.r* – growth ring boundary; *n.t* – narrow tracheids; *r* – ray; *w.t* – wide tracheids.

have 1 to 6 bordered pits to communicate with other tracheids. The remaining 39% of tracheids are also narrow but they only communicate with ray cells (Fig. 18). The narrow tracheids are in the spring wood as well as in the summer wood. However, they are absolutely absent on the very borders between the growth rings. Narrow tracheids in the summer wood outnumber those in the next spring wood by nearly 8%.

Most of the wide tracheids of ginkgo's SVW have bordered pits in their radial walls, though the outmost summer wood tracheids and adjoining innermost spring wood ones of the next growth ring have rather numerous bordered pits in their contiguous tangential walls. These bordered pits principally enable communications between consecutive growth rings. Additionally, the tracheids are curved inwards on both ends. Thereof, the wide spring wood tracheids intrude into the mass of their summer wood counterparts of the preceding growth ring with their terminal parts. Contiguous (parts of) radial walls appear where the spring wood tracheids overlap the summer wood tracheids. These (parts of) radial walls bear bordered pits which allow communication of summer wood tracheids with the spring wood tracheids of the next outer growth ring (Fig. 19).

The narrow tracheids of ginkgo's SVW are mostly grouped into irregular tangential bands which alternate with similarly structured bands of the wide tracheids in every growth ring (Fig. 20). The shapes and locations of the bands of narrow tracheids change along the stem. Few solitary

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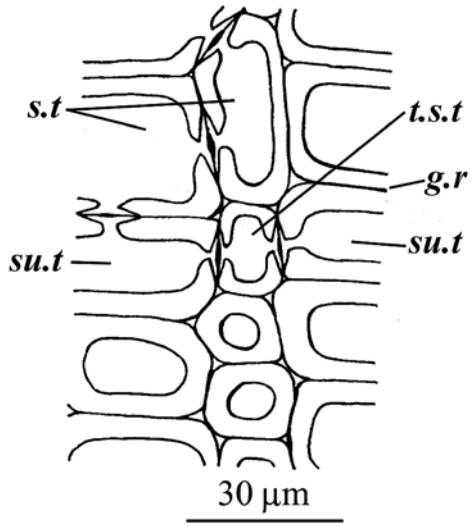

Figure 19. Summer / spring wood boundary in SVW of *Ginkgo biloba* L. *g.r* – growth ring boundary; *s.t* – spring wood tracheids; *su.t* – summer wood tracheids; *t.s.t* – terminal part of spring wood tracheid intruding into the mass of summer wood tracheids.

narrow tracheids seen in some cross-sections of the wood are always in contact with band/s above/below the cross-section level. The narrow tracheids of a growth ring are thus arranged into a 3D net of strengthening constituents of the wood. Such a net does not stretch across the growth ring boundaries, because the very early spring wood practically has no narrow tracheids. As a result, every growth ring has an isolated 3D system of strengthening constituents[3].

Wide tracheids are filled with xylem sap, while nearly all narrow tracheids contain gas, irrespective of whether they communicate with other tracheids by means of their bordered pits.

The design of strengthening constituents of ginkgo's SVW is quite different from that of other SVWs, but it is rather similar to the diffuse growth ring design of SHWs in some woody dicotyledons. Indeed, repeatedly alternating bands of narrow and wide tracheids in growth rings of ginkgo's SVW (Fig. 17 B) highly resemble alternating tangential/oblique tangential bands of vessels and libriform fibers/fibrous tracheids of some to all members of dicotyledonous Araliaceae, Calycanthaceae, Pittosporaceae, Platanaceae, Proteaceae (Fig. 17 C), Ulmaceae etc. (Metcalfe & Chalk 1950). However, the circular growth ring design of gingko's SVW is also distinctive (Figs 17 B, 18). Thus, combined circular and diffuse growth ring designs of SVW have evolved in ginkgo just as in dicotyledons with SHWs, but ginkgo has not developed vessels.

Gas fills narrow tracheids of ginkgo's SVW and summer wood tracheids of pine's, larch's and spruce's SVWs as well as libriform fibers of maple's and ash's SHWs in a short period of time after developing from cambial derivatives. Consequently, not only libriform fibers of angiosperms (Braun 1963) but also strengthening tracheids of ginkgo, pine, larch and spruce are predetermined to be filled by gas. Such a gas is a by-product of vital functions of cells of the wood parenchyma (Kramer & Kozlowski 1960, 1979).

Living constituents of wood

Ray parenchymal cells and axial formations like axial parenchyma, fusiform parenchyma and living libriform fibers are all living constituents of the secondary wood. German xylotomists (Troschel 1879; Krah 1883; Gnentzsch 1888; Jahn 1894) revealed in late 19th century that every strand of the axial parenchyma always contacted another strand/s and/or ray/s even if the axial parenchyma was diffuse and very scanty. Their data provoked later xylotomists to consider that all living constituents of the wood are united within a continuous 3D system

3) The bands of the wide tracheids also change along the stem and anastomose each other. They totally constitute a continuous 3D net of conducting tracheary elements which spreads all over the wood, because it is not discontinuous on the growth ring boundaries.

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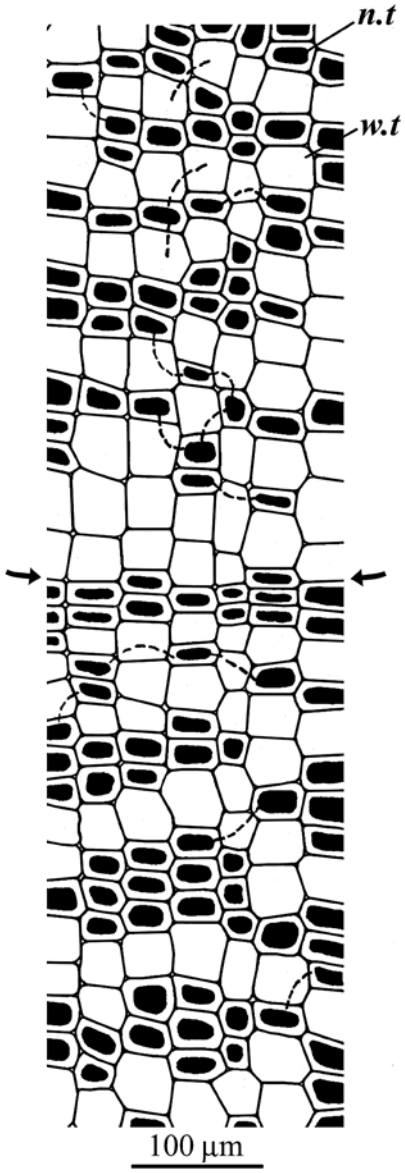
(Fig. 21). However, there are SVWs, for instance those of some species of *Araucaria* and *Agathis* (Kisliuk 1959), which have no longitudinal living constituents but rays. The latter are nearly strait unbranched radial strands. Therefore, they are unable to anastomose. Every ray is thereof completely isolated by the mass of dead tracheids. Then, these SVWs have no continuous 3D system of living constituents but separated rays. Such a system arose in progressing wood after axial parenchyma had evolved.

1355 strands of the axial parenchyma have been traced in wood samples of *Fitzroya patagonica* Hook. f., *Alnus incana* (L.) Moench, *Populus tremula* L. and *Fraxinus excelsior* L. which differ in arrangements of living constituents of their SHWs (Fig. 22). None of the strands was absolutely isolated from other living constituents. The vast majority of the strands directly contact one to several (up to 10 in *Fitzroya*) rays. There are also axial parenchyma strands in the SHWs of alder, aspen and ash that do not contact rays but other strand/s. The living constituents of the investigated SHWs intercommunicate by pits in their contiguous walls. I have termed such walls '*contact walls*'. The more numerous pits contact walls bear, the more advancely the living constituents of a wood intercommunicate.



The axial parenchyma strands mostly contact rays by the radial walls of their cells (Fig. 23 A), which always have numerous pits (Fig. 24 A–C). Rather many axial parenchyma strands, especially in alder and aspen, adjoin the rays from above/below by their terminal cells. Then, the contact wall between an axial parenchyma cell and a ray cell only bears 1–2 pits due to the small area of the wall (Fig. 23 B). The axial parenchyma strands mostly contact each other by the radial walls of their contiguous cells. Accordingly, the tangential walls of these cells have much less numerous pits than the radial ones, if any (Fig. 24). If separated from the ray by non-living constituents of the SHW, the axial parenchyma strand sometimes protrude towards the ray. The latter also protrudes towards the strand. The contact between both protrusions allows direct communication between axial and ray parenchyma (Fig. 25 B). Similar protrusions directed to each other are rarely intercommunications between adjacent axial parenchyma strands (Fig. 25 A). Such protrusion contacts clearly show the importance of direct communications between living constituents of wood.

Figure 20. Patterns of narrow and wide tracheids in the cross-sectioned SVW of *Ginkgo biloba* L. *n.t* – narrower thin tracheid; *w.t* – wider thick tracheid; *arrow* – growth-ring boundary; *dotted line* – intermediated communications between the tracheids.

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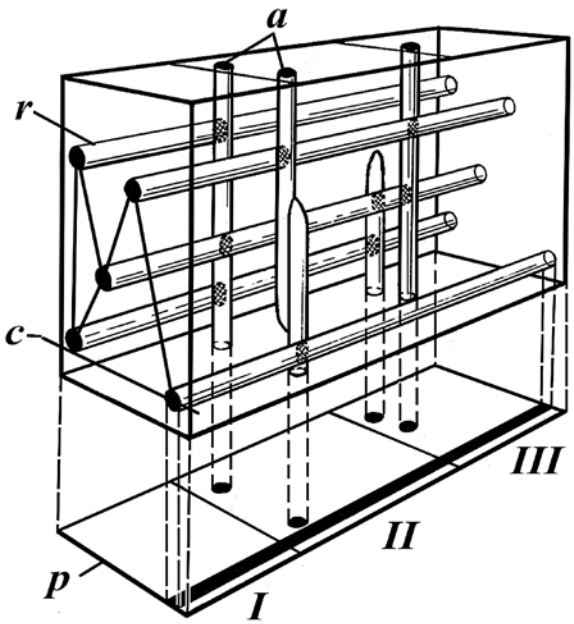

Figure 21. 3D diagram of living constituents of SHW sample in *Fitzroya patagonica* Hook. f. *a* – axial parenchyma; *c* – level of the cross-section projected below in 'p'; *p* – projection of the 'c' cross-section; *r* – ray; *I–III* – growth rings.

Thus, radial contact walls principally enable intercommunications of living constituents of the wood while another contact walls are only accessorial.

The axial parenchyma connects all rays of trunk SHWs tangentially and longitudinally in the four above mentioned species and also in *Ficus carica* L. The connectivity of their rays varies, however, depending on the patterns of the axial parenchyma and its quantity. The diffuse (*Fitzroya*) and diffuse metatracheal (alder) axial parenchymas both result in zigzag connections between rays, viz. the longitudinal connections deviate radially and the tangential connections deviate radially and longitudinally (Fig. 26). Terminal axial parenchyma (aspen) mostly results in straight longitudinal and tangential interconnections of rays. Every ray interconnection is just straight if either terminal or metatracheal axial parenchyma is combined with the paratracheal one (ash, fig tree). Distinctive paratracheal axial parenchyma alone results in straight longitudinal interconnections with rays while tangential interconnections of the latter are rather zigzag. More voluminous axial parenchyma and bigger tangential masses of it result in straighter longitudinal and tangential interconnections of the rays and in more reiterative ray interconnections. Straighter and more reiterative ray interconnections lead to more integrated rays.

Radial continuity of living constituents of the wood is mainly kept by the rays while their longitudinal and tangential continuities are kept by the axial parenchyma. Quantity and patterns of the latter cause connectivity of rays and determine relative contributions of the rays and axial parenchyma to keeping 3D connectivity of the living constituents of the wood. More voluminous axial parenchyma and its larger longitudinal and tangential masses lead to prevailing of the axial parenchyma over the rays in maintaining longitudinal and tangential integrity of the living constituents of the wood. Moreover, not only the rays but also the axial parenchyma takes part in maintaining radial continuity of the wood living constituents, especially if this parenchyma is rather voluminous and arranged in large masses.

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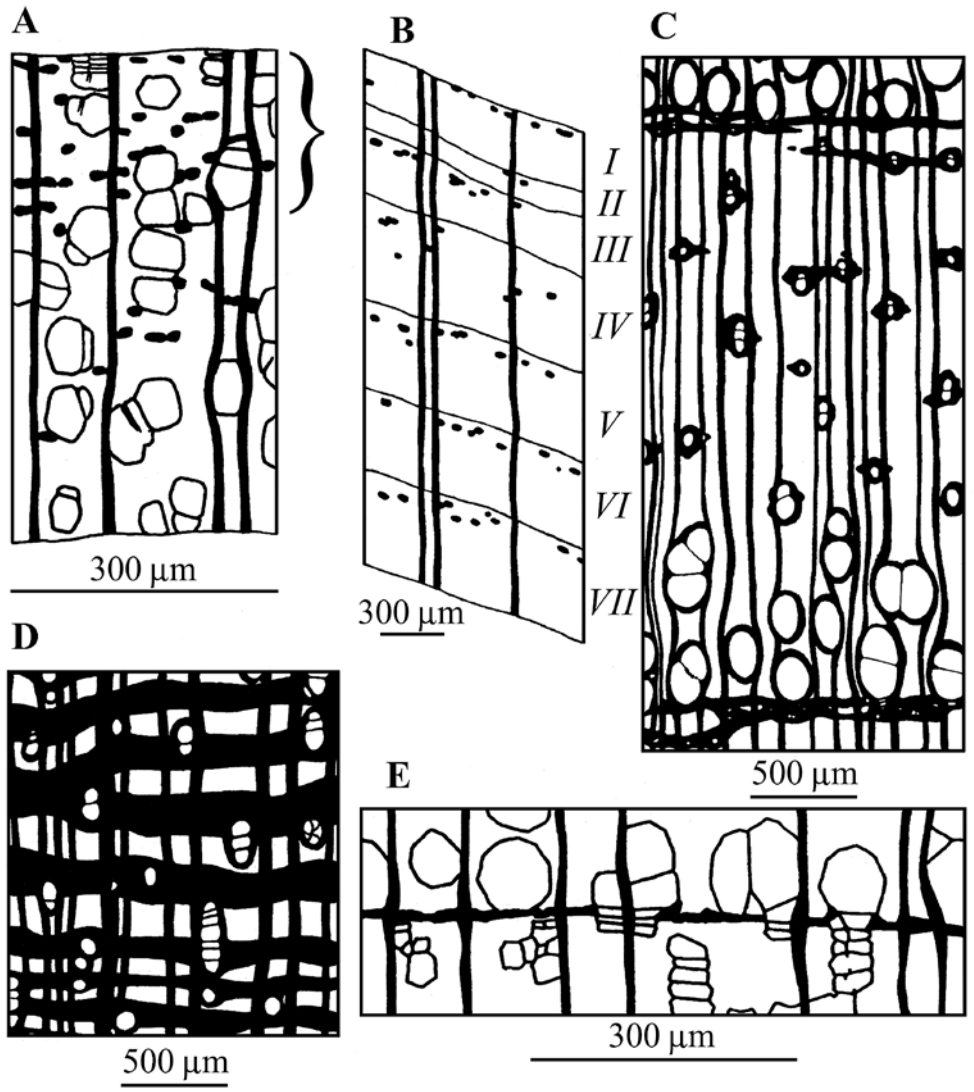

Figure 22. Patterns of the living constituents of the cross-sectioned SHWs. A – *Alnus incana* (L.) Moench; B – *Fitzroya patagonica* Hook. f.; C – *Fraxinus excelsior* L.; D – *Ficus carica* L.; E – *Populus tremula* L. *Brace* – outer ⅓ growth ring; *I–VII* – successive growth rings.

Plant anatomists (Grebnitskiy 1884; Haberlandt 1904; Peretolchin 1904; Borodin 1910; etc.) already considered in late 19th and early 20th century that living constituents of wood fulfilled a storage function. Jeffrey (1917) believed that the axial parenchyma had evolved to enlarge nutrient reserves in the wood which had been necessary under seasonal climates. The terminal axial parenchyma was thought to have arisen at first (Jeffrey 1917; Takhatjan 1948). It improved nourishing spring wood under development at the beginning of the growing season. However, tropical trees are well known to have much more voluminous axial parenchyma in their woods than their counterparts of temperate climates (Brown & Panshin 1940; Wagenführ 1966). Quite the opposite should be expected, because the deciduous trees of temperate climates certainly need more reserve substances in their woods to start thickening in early growing season than the evergreen tropical trees need. Besides, the axial parenchyma cells have pits mostly in their radial walls while their tangential walls are nearly pitless. These pitted radial walls enable direct

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communications between strands of axial parenchyma as well as between the axial parenchyma and the rays, but they communicate neither with cambium nor with developing spring wood. Therefore, the nutrients stored by the terminal axial parenchyma are evidently transferred to the cambium zone by the rays. Thus, the terminal axial parenchyma could be interpreted as a container of reserve material which is unable to nourish the cambium zone directly. If so, it is unclear why the axial parenchyma evolved to enlarge capacity of living constituents of wood for advancing storage function of the wood. Indeed, the rays had arisen in woods long before the terminal axial parenchyma evolved. If ray number, ray size or both had increased, the capacity of living constituents of wood for storing nutrients would have been easily enlarged and the storage function of the wood would have improved without evolving a terminal axial parenchyma.

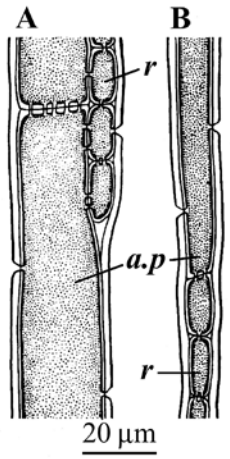

Figure 23. Contacts between axial and ray parenchyma of the SHW of *Alnus incana* (L.) Moench. A – lateral contact of the axial parenchyma strand; B – terminal contact of the axial parenchyma strand. *a.p* – axial parenchyma; *r* – ray.

Bower (1930) pointed out that evolutionary increasing of plant sizes had indispensably caused increasing of the specific volume of wood in their bodies. If wood had consisted of only tracheids, the interfaces between the living cells and the tracheids would

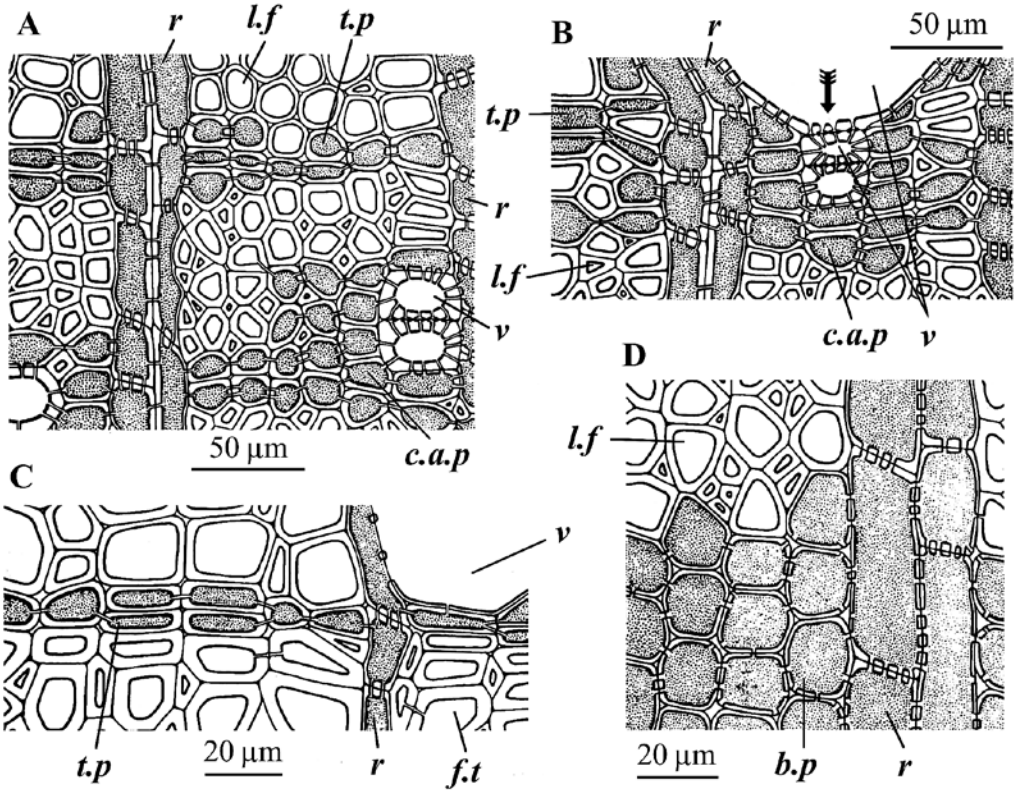

Figure 24. Cross-sectioned SHWs. A, B – *Fraxinus escelsior* L., growth ring boundary; C – *Populus tremula* L., growth ring boundary; D – *Ficus carica* L. *b.p* – banded axial parenchyma; *c.a.p* – confluent aliform axial parenchyma; *f.t* – fiber tracheid; *l.f* – libriform fiber; *r* – ray; *t.p* – terminal axial parenchyma; *v* – vessel; *arrow* – intervascular contact between growth rings.

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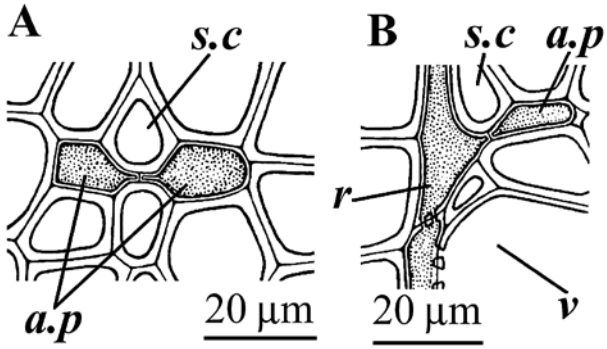

Figure 25. Parenchyma contacts in the SHW of *Alnus incana* (L.) Moench, cross-sections. *a.p* – axial parenchyma; *r* – ray; *s.c* – strengthening constituent of the SHW; *v* – vessel.

drastically have been reduced to a minimum. Evolutionary development of living constituents of wood, i.e. rays as well as axial parenchyma, and their subsequent progress were thought to have compensated this interface reduction. Bower (1930) also believed that a certain area of these interfaces would be necessary to maintain enough metabolic interacting between living constituents of wood and non-living ones. Bannan & Bailey (1956) revealed that every fusiform initial cell of the cambium contacted few sets of the ray initial cells of the cambium. Then, every tracheid of the SVWs is long enough to contact living cells (of few rays), irrespective of whether there is axial parenchyma in the wood. The same is even more feasible for much longer vessels

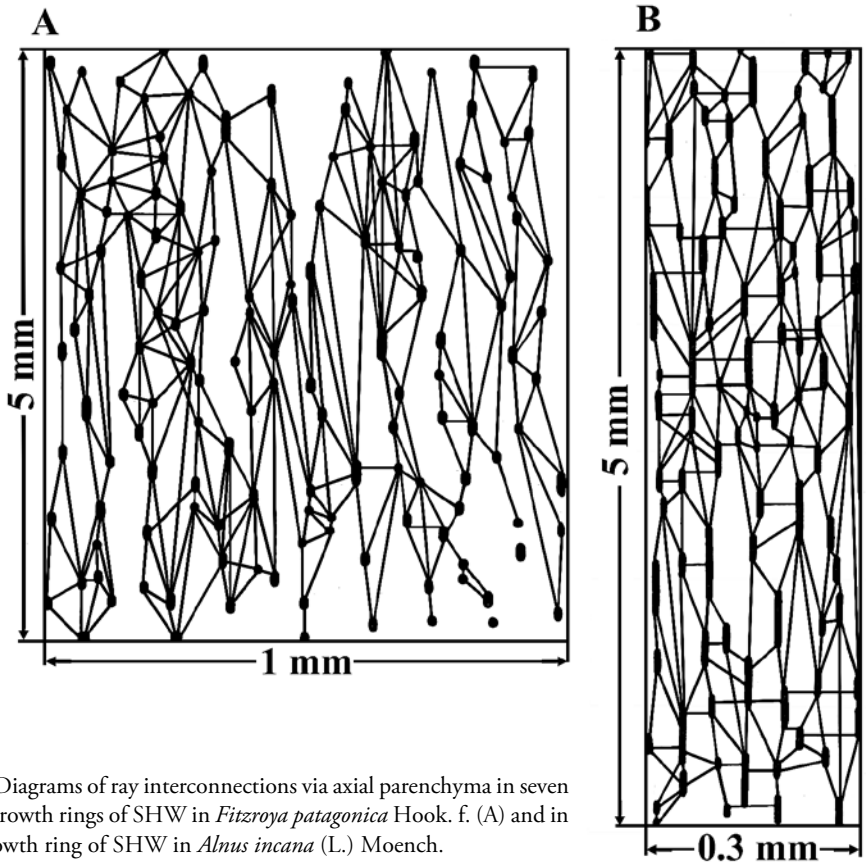

Figure 26. Diagrams of ray interconnections via axial parenchyma in seven successive growth rings of SHW in *Fitzroya patagonica* Hook. f. (A) and in outer ⅓ growth ring of SHW in *Alnus incana* (L.) Moench.

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of the SHWs. Therefore, the required interface area between the tracheids/vessels and the living constituents of wood would have maintained by means of progressing rays without the arising of axial parenchyma. Evolutionary development of the axial parenchyma has thus to be explained.

Some physiological experiments have shown that mineral substances are quite easily and rapidly transferred bidirectionally between the wood and the bark (Stout & Hoagland 1939; Chen 1951; Ratner et al. 1959). Undoubtedly, the rays conduct these substances. Therefore, the rays and any living constituent of the wood are worth being considered as special conducting systems. The latter are also able to conduct substances longitudinally and tangentially, because it is a continuous 3D system when the axial parenchyma is present. Such a system must conduct substances rather independently of the transpiratory water current through the wood. If so, the substance current must be quite independent of highly changeable environmental characters that directly influence the water current. Moreover, the 3D living system of the wood can conduct substances in the opposite direction to the water current in the tracheids/vessels. The axial parenchyma may have evolved to convey substances independently of the water current in its tracheal elements. Once the axial parenchyma had evolved, it also performed storage function and it increased the areas of interfaces between living constituents of wood and tracheids/vessels.

Transpiratory waterflow outward the xylem in the leaves leads to hydrostatic tension of the water filaments in tracheal elements of wood which causes collapsing forces in the walls of these elements. In definitive SHWs, these forces are resisted by robust walls of the vessels and also by wood constituents which form a tightly joined (by means of shared cell plates) sheath around the vessels. Such sheaths thus strengthen the vessel walls. The vessel sheaths of ash mostly consist of the vasicentric axial parenchyma but also rays and some libriform fibers take part in sheathing. The axial parenchyma strands adjoining vessels differ from those isolated from the latter because they consist of distinctively shorter cells (Fig. 27 A, B). The transverse cell walls of the vasicentric parenchyma as a whole gird the vessels like sets of tension braces (Fig. 28) which are functionally analogous to circular and spiral thickenings of the cell walls inherent in protoxylem vessels. The shorter vessel-sheathing cells result in more numerous 'tension braces' per a vessel-length unit to make the vessel more resistant against collapsing forces. There are also rather numerous transverse cell walls joining the vessels where they are contacted by rays, because rays of ash consist of procumbent cells with small diameter (Fig. 27 C).

It would be wasteful to make vessel walls more collapse-resistant by means of increasing their thickness. Indeed, very thick vessel walls would be effectual only in the developing wood. In the definitive wood vessel-sheating cells prevent vessels from collapsing to a greater extent which make very thick vessel walls unnecessary. Besides, the vessel segments would have to remain alive for a rather long period of time to develop thick walls. Then, their conducting function inevitably has to be delayed in this period of time. Vessels of early wood keep functioning for only 1–1½ growing season in most ring-porous trees. Such trees have scanty conducting vessels, if any, at the beginning of the growing season, because those produced in the preceding season are mostly blocked by tyloses. That is why the rapid development of the spring wood vessels must take place before foliation in the ring-porous trees to enable them to start growing in spring (Huber 1935).

Vessels start conducting water 10 days after their initiation in ash wood. The beginning of vessel operating is always preceded by the complete development of vessel sheaths. Spring wood vessels synchronously develop with foliation, so the spring wood progresses when the tree does not have

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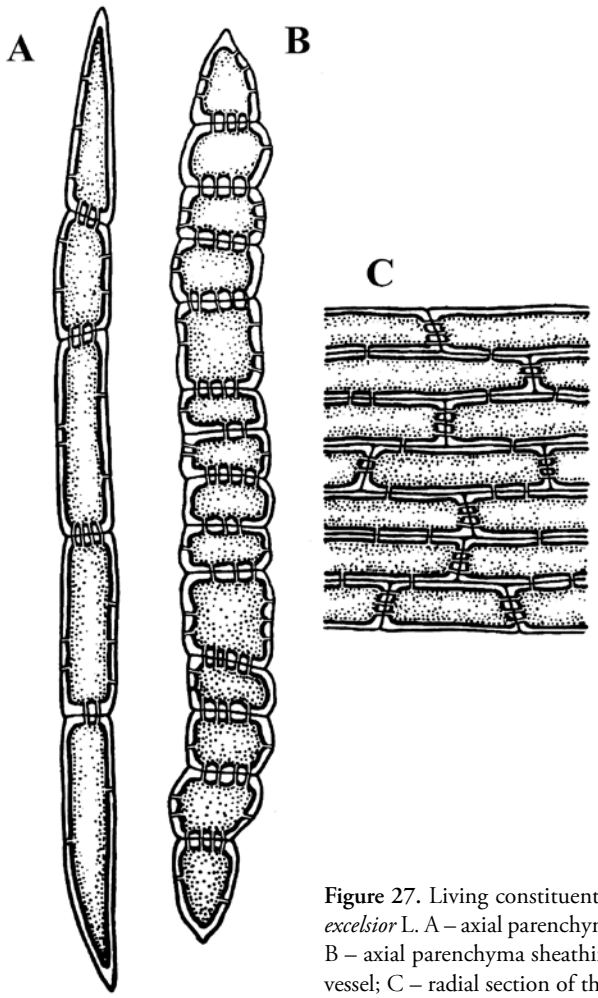

Figure 27. Living constituents of the SHW of *Fraxinus excelsior* L. A – axial parenchyma isolated from the vessel; B – axial parenchyma sheathing vessel, viewed from the vessel; C – radial section of the ray.

photosynthesizing leaves yet. This means that developing early wood consumes stored reserve nutrients and competes with foliation in using them. Therefore, this wood is restrictedly supplied with nutrients only to develop the vessels and their sheaths that are absolutely essential at the beginning of growing season. Other inner derivatives of the cambium remain underdeveloped for rather long period of time. Thereof, in the early growing season the spring wood of ring-porous trees consists of bulky underdeveloped insufficiently strong wood constituents and sparse operating sheathed vessels. The latter are gradually added by newly formed sheathed vessels which differentiate from the underdeveloped constituents in between. A complete ring of wide spring wood vessels thus arises in the increasing growth ring of the wood. Non-sheathed constituents of the spring wood differentiate after the foliage has developed and cambium has started to produce the summer wood. They use nutrients supplied by the operating foliage for their developing.

The spring wood vessels have 1-layered sheaths by the time they start operating. The sheaths incorporate other wood constituents later on to thicken up to 3–4 cell layers. This kind of progressing of sheaths can be called 'vesselfugal'. The sheaths thereby become stronger and harder to withstand increasing collapsing tensions in vessel walls which are caused by the increasing suction of progressing foliage.

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Vesselfugal development of wood constituents is also inherent in diffuse-porous trees, though it is indistinctive and manifests as anticipating lignifications of cell walls. In ring-porous trees, vesselfugal development of wood constituents is quite conspicuous (Lobzhanidze 1958, 1961) because the vessel sheaths highly anticipate other wood constituents. Such a development of wood constituents is of great importance for ring-porous trees, because their vessels conduct water for only 1–1½ growing season. Accordingly, nearly the whole water needed for transpiration is conducted by the latest growth ring of the wood. Only few spring wood vessels of this ring keep this water current. On the contrary, the vessels in diffuse-porous trees keep functioning for dozens of years and several to many growth rings simultaneously conduct water (Huber 1935; Kozlowski & Winget 1963; etc.). Therefore, the foliage suction dissipates through a lot of functioning vessels in the diffuse-porous woods. As a result only a slight collapsing tension arises in each vessel of the developing wood. Because there are much fewer functioning vessels in the latest growth ring of ring-porous wood, each vessel gets stressed by higher foliage suction. This results in a much higher collapsing tension generated in the vessel walls. Besides, the vessels of ring-porous woods are usually wider than those of diffuse-porous woods (Huber 1935). Wider vessels have less collapse resistance. That is why the vessels of ring-porous woods need a rapid strengthening by vesselfugal sheaths to withstand successfully the greater collapsing tension.

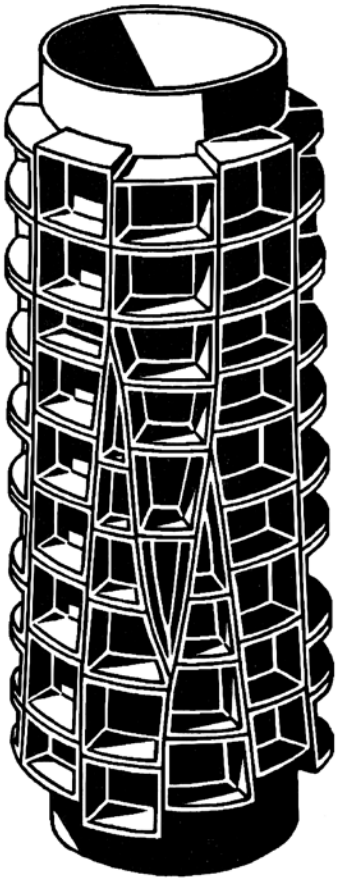

Figure 28. Diagram of the parenchyma sheath of the vessel in SHW of *Fraxinus excelsior* L.

Thus, the few conducting vessels in the ring-porous woods have to develop rapidly and to start functioning before foliation which produces then enough nutrients for a synchronous developing of all other spring wood constituents. This causes a conspicuous vesselfugal differentiation of the vessel sheaths in progressing spring wood in ring-porous trees.

Wood evolution

Several evolutionary trends of various characters of wood were revealed by many scientists (e.g., Bailey & Tupper 1918; Frost 1930a, b, 1931; Kribs 1935, 1937; Gilbert 1940; etc.). These trends were summed up to the 'wood advancement code' (Yatsenko-Khmelevskiy 1948, 1954b; Takhtajan 1947, 1966). Rather many codified characters seem to have progressed correlatively, though their correlations are only statistically noticeable. For instance, there are 20% species with paratracheal axial parenchyma and 5% ones with homogeneous rays among the trees that have primitive scalariform perforation plates in their vessels (Chalk 1937, 1962). Both paratracheal axial parenchyma and homogeneous rays are considered advanced characters. Quite the reverse occurs in trees with highly advanced simple perforation plates and storied wood constituents: 10% have primitive solitary vessels, 10% have clearly bordered pits in the walls of strengthening

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constituents and 25% have diffuse axial parenchyma (Chalk 1937, 1962). These characters are considered as primitive. Chalk's data thus show that these characters are not directly integrated; otherwise they would be correlated.

Differently advanced characters of the wood can be combined within a species. This phenomenon has been termed 'evolutionary heterochrony of characters' (Kozo-Polyanskiy 1940; Takhtajan 1946) or 'evolutionary heterobathmy of characters' (Takhtajan 1966). As a result, routine reconsidering of separate evolutionary pathways of different wood characters need to be replaced by realizing the evolutionary progressing of the integral wood.

Secondary wood results from cambial activity. The cambium is believed to have evolved several times and independently in different taxa of higher plants (Bower 1930; Barghoorn 1964; Lebedenko 1976; etc.) to increase conductivity of plant vasculature (Bower 1930; Bailey 1953). The cambium is invariably a derivative of the procambium. Thereof, it is reasonably thought to have originally produced the tracheids that were quite similar to those of the metaxylem. The latter are well known to have numerous bordered pits in every contiguous wall between tracheids. Then, the tracheids of SVWs must originally have born numerous bordered pits in all their contiguous walls. The tracheids do have abundantly pitted radial and tangential walls in SVWs of lepidodendrons and cycads. This means that SVWs of these plants have not been subjected to the increasing of strength during their evolution. These SVWs thus retain original structure.

Abundant bordered pits in all tracheid walls weaken the tracheid. That is why the SVWs must originally have been an exclusively conducting tissue just as the primary xylem is. As a result, mostly the peripheral extra-xylem tissues of a stem make it strong.

Once the SVWs had arisen they were gradually taking over more strengthening function because they evolutionary increased their specific bulks. The SVW has become the only tissue that maintains water-conducting and strengthening functions in pycnoxylic trees. Structure of such a SVW must equally fit these two functions, i.e. the SVW must be sufficiently conductive and strong enough. The conductivity of SVW is determined by diameters of tracheid lumens and by numbers of the bordered pits which interconnect contiguous tracheids. The strength of the SVW depends on the thickness of the tracheid walls and on areas of conjoint solid parts of the walls of contiguous tracheids. In the beginning of SVW evolution the primitive SVWs were increasing areas of solid (unpitted) parts of tracheid walls to become stronger (Bailey 1953; Yatsenko-Khmelevskiy 1954b).

The bordered pits in the tangential walls of tracheids became futile for longitudinal water-conductance of the SVWs, because the tracheids had been situated in radial rows. The longitudinal water current in the SVW ran thereof through bordered pits in the radial walls of tracheids. These pits were also able to maintain radial water conduction of the SVW which was probably small due to rather thin SVWs in primitive trees. As a result, neither longitudinal nor radial water conduction deteriorated after bordered pits had been reduced in the tangential walls of tracheids. Thus, initial structure of the SVW constituents changed very effectually, when solid tangential walls of tracheids evolved which made the SVW much stronger without diminishing its water conductivity.

The SVWs of manoxylic trees are of minor importance as strengthening tissues. Nevertheless, most of them have tracheids whose radial walls are pitted throughout, while the tangential ones

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bear scanty bordered pits, if any. Then, number of the bordered pits in the tangential walls of tracheids must have been reduced first to fit the primitive SVWs for strengthening function. This pit number reducing resulted in complete disappearance of the bordered pits in the tangential walls of tracheids in many SVWs.

The acquired strengthening function of the SVW was subsequently advanced by means of changing the pattern of pits of radial walls between tracheids. Bordered pits of the terminal parts of tracheids were crucial for longitudinal and radial water conduction. Those in the middle parts of tracheids were rather ineffectual. Therefore, reduction of these pits hardly influenced the conductivity of the SVW. Indeed, the pits between middle parts of tracheids disappeared during evolution. In cordaitalean SVWs, the bordered pits took up nearly the whole radial wall except intersections between rays and tracheids (Gothan 1907; Yarmolenko 1933; Yatsenko-Khmelevskiy 1948, 1954b; etc.). In SVWs of modern conifers, they tend to occupy the terminal parts of radial walls of their tracheids. Only after the pattern of pits in radial walls between tracheids had evidently changed, the pits became scanty to absent in the tangential walls of tracheids.

Progressing rhythmical thickening must have caused more distinctive summer wood of tracheids with reduced areas of their radial walls and decreased pit numbers there. Bordered pits certainly reappeared in the tangential walls of these tracheids, however, to compensate this reducing.

Water conductivity of the living constituents of the SVWs, viz. axial parenchyma and rays, is infinitesimal. Thereof, they cannot contact large areas of tracheid walls bearing pits between tracheids for conducting water. Besides, the living constituents of wood are much weaker than the tracheids, so the SVWs containing tracheids and living constituents are weaker than those containing only tracheids. Accordingly, bulky wood parenchyma would highly reduce both strength and conductivity of the SVWs. That is why few uniseriate rays and very scanty diffuse axial parenchyma are inherent in most SVWs requiring minimal specific volume of a wood piece. Only few conifers have more living constituents in their woods, because they produce resin ducts in their SVWs to withstand more efficiently xylophagous and pathogenic organisms.

The SVWs of the dicotyledons were divergently evolving to a water-conducting subsystem and to a strengthening one.

The strengthening subsystem of secondary wood initially consisted of fiber tracheids which progressed to get thicker walls and to reduce size and number of their bordered pits. These characteristics made fiber tracheids stronger than normal tracheids of the SVWs. Cohesion of the fiber tracheids also improved, because the reduction of their bordered pits resulted in increased specific areas of solid parts of their contiguous walls. Strength of the secondary wood thus progressed by means of increasing strength of the fiber tracheids and their cohesion. However, thicker walls of the fiber tracheids caused a narrower lumen. Fewer bordered pits in the fiber tracheid walls led to an impediment of interconnections of the tracheids. The fiber tracheids consequently became less conductive and therefore more water-resistant.

Advancement of the strengthening subsystem of wood would inevitably have reduced wood conductivity, if the water-conducting subsystem had not progressed up to vessels. Evolving vessels were substituting tracheids in maintaining transpiratory water current through the wood. They were thus a prerequisite for progressing the strengthening subsystem of wood. However,

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the tracheids could completely cease water conduction and could change into libriform fibers, only after the direct communications between vessels had evolved. Tracheidal and mixed communications between vessels caused the tracheids to take part efficiently in water conduction and to develop rather numerous distinctive bordered pits in their walls which decreased their strength. The progressing of the direct communication between vessels resulted in releasing the tracheids from water-conducting. Reduction of the pits in tracheid walls thus enhanced the improvement of the cohesion between tracheids and of the whole strengthening subsystem of the SHW. After the direct communications between vessels had highly evolved, all tracheids stopped conducting water and changed into libriform fibers. The functional acme of the strengthening subsystem of the SHW was thus attained.

Increased conductivity of the water-conducting subsystem of the SHWs resulted from raised conductivity of constituent vessels and advanced communications between vessels. The direct communications between vessels were certainly more water-permeable than the tracheidal ones. Then, the former communications evolutionarily replaced the latter ones. This replacement was gradual because SHWs with varying proportion of direct communications between vessels to tracheidal communications exist(ed). Increasing conductivity of the water-conducting subsystem of SHW inevitably caused a decrease of its strength. Indeed, vessel advancing like an enlarged vessel diameter, the transformation of the scalariform perforation plates to simple ones, the reduction of the tails of vessel segments cooperatively resulted in a reduction of vessel strength. The increasing number of intervessel pit pairs led to decreased areas of solid parts of their contiguous walls and consequently to a decreased cohesion of the vessels.

Effectual contacts between vessels and water-conducting tracheids require a rather large area of vessel walls. Characteristically scattered pits in the tracheid walls result in similarly scattered counter-pits in these parts of vessel walls. The diffuse-pitted vessel walls are less water-permeable than the close-pitted ones. Advancing of vessels and their direct intercommunications must have been prerequisites for excluding tracheids from water-conducting. This is evidenced by reduced bordered pits in tracheid walls in SHWs with progressed direct communications between vessels. The reduction of the pits in tracheid walls must have coincided with reduction of their counter-pits in the vessel walls which the tracheids adjoined. The directly communicated (parts of) vessels, especially wider ones, are mostly flattened in the contact plane. Thereof, the areas of the contiguous vessel walls are large enough to bear numerous dense bordered pits. The densely pitted walls of vessels are therefore more water-permeable than those bearing diffuse pits. Closer pits in the contiguous walls between vessels enable them to reduce contact areas between the vessel and other water-conducting tracheary elements.

The water-conducting subsystem and the strengthening one were reciprocally evolving in dicotyledonous SHWs. Indeed, progressing of the strengthening subsystem was just necessary for advancing of the water-conducting subsystem; otherwise, the strength of SHW would have been reduced. Advancing of the water-conducting subsystem was likewise *sine qua non* for progressing of the strengthening subsystem; otherwise the SHW would have become more water-resistant. The evolution of the water-conducting subsystem seems to have been strictly synchronized with that of the strengthening subsystem, because such a synchronism was the only possibility for SHWs to remain equally fitted to fulfill both principal functions of the secondary wood, viz. conducting and strengthening (Fig. 29).

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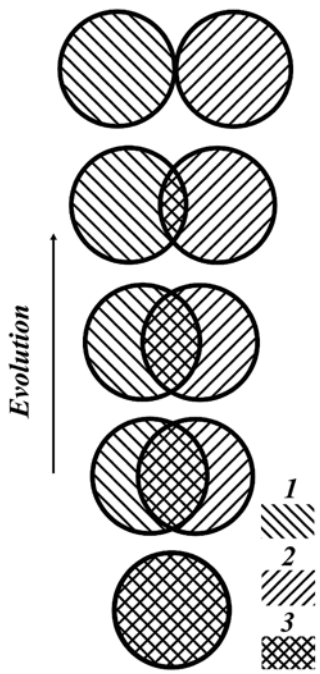
The water-conducting and strengthening subsystems of secondary woods of dicotyledons did not evolve as additions to the tracheidal component of the wood inherent in their ancestors. Instead, both subsystems were progressing to substitute the tracheidal component. Therefore, synchronous advancements of these subsystems were also synchronous with reduction of the latter (Fig. 29).

Divergent evolution of water-conducting and strengthening subsystems of the secondary woods must have depended on the progress of the paratracheal axial parenchyma. Physiology data show a tight physiological association between conducting constituents of the wood and those of the bark (Afanas'eva 1955; Kramer & Kozlowski 1960; etc.). This association is kept by direct contacts between tracheary elements and living constituents of the secondary woods, viz. rays and axial parenchyma.

Every vertical tracheid of the SVW is water-conducting and it contacts ray/s. Thereof, every tracheid thus maintains transpiratory water current and takes part in the physiological association between wood and bark. The bulk of tracheids was specializing its strengthening function when dicotyledonous' SHWs were progressing. These changing tracheids were naturally reducing their original conducting function and physiological association with the conducting constituents of the bark. Then, the vessels were synchronously intensifying their water-conducting function and their role in the physiological association between wood and bark by means of increasing the contact area between vessels and parenchyma via evolving parenchymal sheaths round the vessels. However, these sheaths could adjoin only those parts of vessels that did not take part in direct or tracheidal communications between vessels. If these vessel parts became larger, more parenchyma cells could contact the vessel.

The increasing of the interfaces between vessel and axial parenchyma could only be possible if diffuse pits in vessel walls had been substituted by dense pits to make vessel walls more water-permeable. The dense pits in the vessel walls thus enabled them to reduce their contact area. As a result, rather large areas of vessel walls stopped participating in communications betwen vessels. These parts of vessel walls became accessible to parenchymal sheaths without reducing the conductivity of the SHW. After the vessels had arisen in dicotyledonous SHWs, the paratracheal parenchyma could evolve depending on the divergent evolution of the tracheary elements. The distinctive paratracheal parenchyma developed after the water-conducting and strengthening subsystems of the SHW had been highly advanced.



Divergent evolution of the tracheids of ancestral woods of dicotyledons and progress of the paratracheal parenchyma were certainly interactive evolutionary processes. They seem

Figure 29. Diagram of synchronous divergent evolution of water-conducting and strengthening subsystems of the secondary wood. *1* – water-conducting subsystem; *2* – strengthening subsystem; *3* – tracheidal system/subsystem with equally combined water-conducting and strengthening functions.

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to have been as synchronous as the divergent evolution of the water-conducting and strengthening subsystems of the wood and as the reduction of the tracheids in the secondary wood.

Because the advance of the water-conducting subsystem as well as the strengthening subsystem, the reduction of tracheids and the advance of the paratracheal parenchyma are synchronous evolutionary processes, the evolutionary level of the paratracheal parenchyma is a suitable indicator of the evolutionary level of the divergence of the wood subsystems and the advancement of the whole SHW in dicotyledons. Divergence of these subsystems and advancement of the whole SHW are both measurable by estimating distinctness of the parenchymal sheaths of the vessels. Thus, there is no need to appraise advancement levels of each character of the conducting and strengthening constituents of a SHW to be mechanically summarized for estimating advancement degree of the whole SHW. The advancement level of the parenchymal sheaths of the vessels automatically integrates those of all individual characters of the water-conducting and strengthening subsystems of the wood and indicates the advancement degree of the latter as well as the whole SHW in dicotyledons.

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Appendix 1. List of Kedrov's articles excerpted.

Kedrov G. B. (1965a): Structure and development of the water-conducting system of ash's (*Fraxinus escelsior* L.) wood and some problems of xylem evolution in woody Dicotyledons. – PhD Thesis: Moscow State University. [In Russian]

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Zeitschrift/Journal: Wulfenia

Jahr/Year: 2012

Band/Volume: 19

Autor(en)/Author(s): Kedrov Gorn B.

Artikel/Article: Functioning wood. 57-95