FUNCTIONAL PLANT ANATOMY

Proceedings
of the International Conference,
Dedicated to 90th Anniversary
of Gorn B. Kedrov

МАКС ПРЕСС

MOSCOW – 2013

Gorn B. Kedrov †

ADVANTAGES OF THE NON-STORIED CAMBIUM[2]

There are 2 types of the cambium routinely recognized that strikingly differ in arrangements of their fusiform initials. In the tangential plane, the arrangement of the latter formations is rather irregular in the non-storied cambium; accordingly, they are long overlapped. The fusiform initials of the storied cambium are in distinctive horizontal layers; correspondingly, the initials of the adjacent layers hardly overlap. The non-storied cambium is inherent in all homoxylic woody plants and in rather primitive heteroxylic dicotyledons whereas more advanced ones have the storied cambium. The non-storied cambium thus seems to have evolved into the storied one of shorter fusiform initials.

According to Bailey (1923), different arrangements of the fusiform initials of these cambia result from different modes of initial multiplication. The fusiform initials of non-storied cambium multiply by means of very oblique transverse divisions and both daughter initials intrusively elongate to become as long as their mother initial or longer. The fusiform initials of storied cambium multiply by radial divisions. Both daughter initials do not elongate but grow tangentially to become as wide as their mother initial.

Though developmental causality of different patterns of the fusiform initials of these cambia as well as the evolution from the non-storied cambium to the storied one must be convincing, there is a question still to be solved whether the non-storied arrangement of the cambium initials is only a sign of their (unadvanced) multiplication mode or it fits some special function(s). To tackle this question, the structure of the cambium-produced wood should be taken into account. Principally that of the homoxylic plants is worth being analyzed because such plants have the most distinct non-storied cambium.

In homoxylic plants, every fusiform cambium initial produces a set of vertical tracheids by means of reiterative strictly tangential divisions, while the tracheids hardly elongate if any. That is why all tracheids produced by the same fusiform initial are arranged in a regular radial row

[2] Text of the presentation at XII International Botanical Congress, June 23–30, 1975, Leningrad.

and are thus at the same level. Non-storied arrangement of the fusiform initials results in non-storied arrangement of tracheid rows. Therefore, tracheids of some radial rows are at higher levels than their counterparts of adjacent rows. The tracheids of adjacent rows more or less long overlap. They resultantly have more or less long contiguous (parts of) radial walls.

The vertical tracheids of homoxylic plants are well known to have bordered pits mostly in their radial walls. There are only summer-wood tracheids that mostly bear bordered pits in their tangential walls, though those are rather sparse there. Thereof, tracheid lumens of the adjacent tracheid rows efficiently intercommunicate directly through numerous bordered pits in their contiguous radial walls, whereas tracheid lumens of the same tracheid row typically intercommunicate indirectly.

The Figure A shows tangential section of a model homoxylic wood of tracheids whose radial walls are evenly pitted. Such a tracheid pitting is characteristic of e.g. cycads. Every bordered pit is clearly seen to connect directly tracheid lumen with the next upper one. Therefore, every bordered pit of radial walls maintains upward transpiratory water flow through the wood. If all tracheid pits had been only in their tangential walls, only tracheid lumens of the same radial row of tracheids would have been intercommunicated by the pits whereas tracheid lumens of the adjacent rows would have completely been isolated. Such a pitting would enable the wood to transfer water radially through the tracheid rows but it prevents the wood from conducting water upward, because all tracheids of a row are at the same level. Then, there are only bordered pits in tracheids' radial walls that maintain transpiratory water current through the homoxylic wood. That is why the tracheids mostly have radial pitted walls in these woods.

If the mode of multiplication of fusiform initials were changed to result in storied cambium, the latter would produce storied radial rows of the tracheids which would hardly overlap (Figure B). The vast majority of the bordered pits in tracheids' radial walls could easily transfer water tangentially in this case, but they would be futile for conducting water upwards, because the tracheids of the adjacent rows would occupy the same level. Therefore, only bordered pits located at tiny overlapped end parts of tracheids would maintain transpiratory upward water-current. As this end part would be too small, the homoxylic wood of storied tracheids would be highly resistant to the transpiratory water flow.

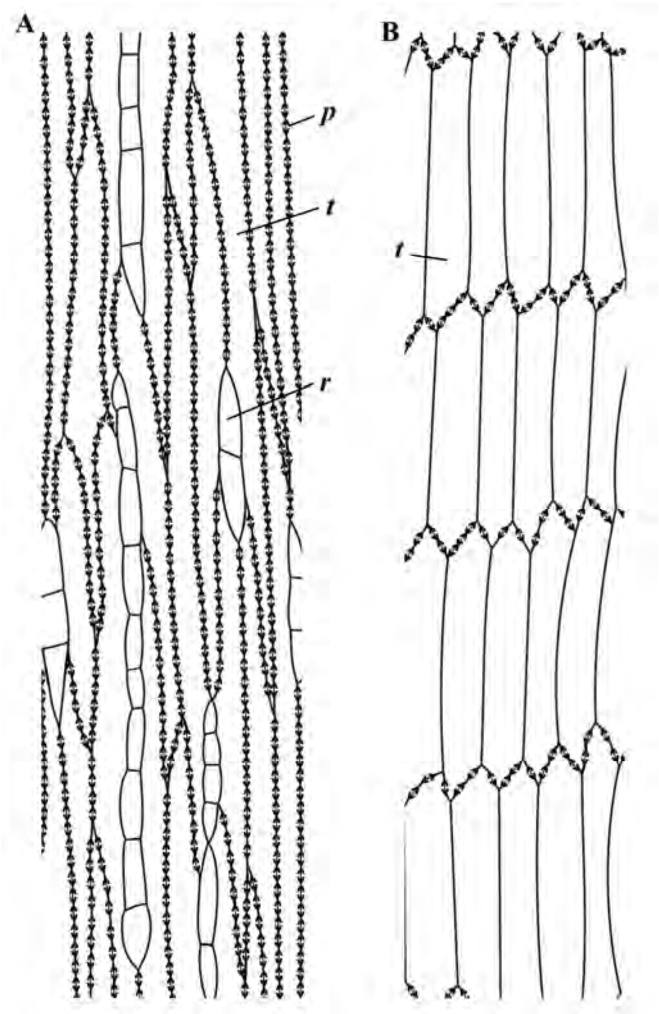

Figure. **Tangential sections of homoxylic secondary woods.**
A – some real wood; B – imaginary wood: *p* – bordered pit; *r* – ray; *t* – tracheid

Longitudinal conductivity of the homoxylic wood could be recovered in this case either by increasing total tracheid number or by considerable intrusive growing of developing tracheids. The former way would require additional resources and give rise to too bulky tracheid lumens which would be superfluous for supplying foliage with necessary water. The way under consideration thus would be too resource consuming and wasteful.

The considerable intrusive growth of developing tracheids would increase overlapping of the leveled tracheids and thus increase number of level-to-level pit connections between the tracheids. However, intrusively overlapped tracheids need much larger tangential room. Thereof, considerable intrusive growth of developing tracheids would inevitably cause too rapid lengthening of xylem girth which would result in too rapid elongation of cambium girth and too intense multiplication of cambium initials as well as too rapid stretching and destroying of the phloem. In reality, the cambium girth elongates rather slowly. Therefore, the considerable intrusive growth of the developing tracheids would be impossible unless the latter would become about twice thinner. However, according to Poiseuille's law, the conductivity of a tube is proportional to its R^4. Thus, twice thinner tracheid is nearly $^1/_{16}$ conductive. That is why the intrusive growth of the storied tracheids must not be a proper way to recover wood conductivity. This would need at least 16 times more tracheids per wood unit.

The firm cohesion of the tracheids is indispensible for the wood to perform efficiently its supporting function. The larger the tracheid contiguous walls are the stronger tracheid cohesion is. Shortly overlapped storied tracheids would have small-areal level-to-level contiguous walls. Shortly overlapped end parts of storied tracheids would thus constitute weak layers in the wood. Such layers would even become weaker because of tracheid pitting typical of many conifers. Their vertical tracheids mostly bear bordered pits in their end parts. This is believed to be a result of evolutionary decreasing of the pit number per a tracheid as caused by advancing the supporting function of the wood. Indeed, the pits make tracheid walls weaker. Densely pitted small-areal end parts of the storied tracheids would thus make tracheid layers easily separable.

Densely pitted end parts of the non-storied tracheids constitute radial rows which are scattered through the wood. Thereof, there are no continuous weak layers in the latter. Besides, the tracheid cohesion is firmer due to their longer overlapping.

There are only non-storied tracheids that enable the homoxylic wood to perform efficiently its conducting and supporting functions. Such a tracheid arrangement would result either from considerable intrusive growth of storied tracheid mother cells or from non-storied fusiform initials of the cambium. The first way has been shown to be too inefficient to have realized in real homoxylic woody plants, whereas non-storied fusiform initials must perfectly be fitted to make non-storied arrangement of the tracheids. Non-storied tracheid arrangement seems to be an evolutionary constraint which has prevented evolution from non-storied cambium to storied one in homoxylar woody plants.

References

Bailey I.W. 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium // Amer. J. Bot. V. 10. P. 499–509.

Gorn B. KEDROV †

DESICCATION-INDUCED DISPLACEMENTS OF THE TORI IN CONIFERS' WOODS (DECIPHERED PROTOCOLS)[3]

Tangentially sectioned spring woods of the latest growing rings were used in all experiments. The woods were sampled from the trunks of living trees in Moscow Region and immediately put into water to prevent them from desiccating. Wet wood samples were 30 μm thick sectioned tangentially with slide microtome. The sections were stained before being manipulated or thereafter. For pre-manipulation staining, the sections were processed either with the aqueous Chrysoidin or with aqueous Water Blue for 7 minutes, differentiated with ethyl alcohol and then 3 times watered. For post-manipulation staining, the sections were processed with ethyl-alcoholic Water Blue for 7 minutes. Two water drops per 100 ml solvent were added, because anhydrous alcoholic Water Blue did not stain tori. These different staining techniques did not influence results of the experiments.

Locations of the tori were detected with the light microscope under magnification 480×.

In every section, nearly all tori were originally flat, thin, unlignified and undisplaced, viz. nearly each torus was just in the middle of paired pits.

---

[3] Kedrov extensively investigated torus displacements in variously influenced conifers' woods for planned major article about torus functions in 1976–1981. The article was not prepared. Rather many protocols of experiments have remained, but only 7 ones are decipherable. They are presented here.