FUNCTIONAL PLANT ANATOMY

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

МАКС ПРЕСС

MOSCOW – 2013

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BIOLOGICAL SIGNIFICANCE OF TRANSVERSE DIVISIONS OF THE FUSIFORM INITIALS OF NON-STORIED CAMBIUM NEAR ITS DESTROYED PART[1]

The fusiform initials of non-storied cambium are nearly parallel to the stem/root axis (Fig. 1, p. 20). They are interlocked by their end parts for rather long parts of their lengths. These cells mostly divide strictly longitudinally by tangential cell walls to give rise to cell pools for the secondary xylem and secondary phloem, respectively. Infrequent ca. 60˚ oblique pseudotransversal divisions of the fusiform initials also take place. They result in multiplication of these cells for continuous cambium to be maintained whereas its circumference gets longer due to outward shifting of the cambium which is caused by inward producing of the secondary xylem by the cambium (Esau, 1953; Fahn, 1967). Injury of the cambium triggers reparative processes. Intense production of the fusiform initials near the damaged part of cambium is among these processes. Orientations of the fusiform cell divisions change in the case of cambium reparation, however. Typical oblique multiplicative divisions of the mother fusiform initials are substituted by approximately transverse ones (Fig. 2, p. 20) (Hejnowicz, 1961, 1963). The present investigation is aimed at revealing biological significance of the above-mentioned re-orientation of the cambium fusiform initial divisions in case of cambium repairing.

Materials and methods

Trunks of young trees of *Picea abies* (L.) Karst. and *Pinus sylvestris* L. were treated in mid June as follows. Some trunks were half sawn and others were semi-circumferentially debarked. The cambium near the wounds was sampled in late growing season of the next year to be examined in tangential sections. The structure of the cambium and its likely change during the interval between injury and sampling were reconstructed by scrutinizing serial tangential sections of the secondary wood produced by these cambium samples. Such a reconstruction is relevant because wood constituents in conifers virtually retain sizes, shapes and tangential-plane orientations their mother cambial initials had. Then, the

[1] Restored presentation at meeting of the Botanical section of Moscow Society of Naturalists, on December 13th, 1972.

tangential sections of the examined wood samples were considered images of the cambium at the moment these parts of the wood were produced.

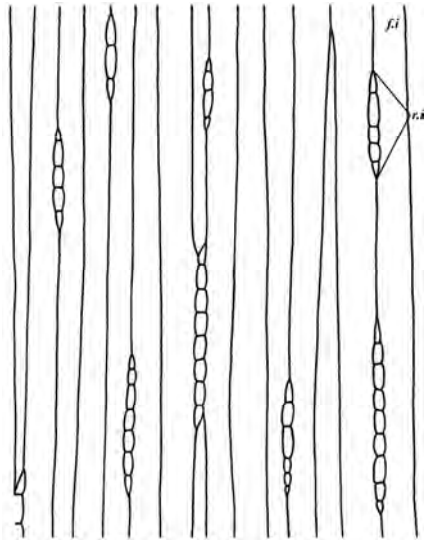

Fig. 1. **Intact cambium, tangential section:** *f.i* – fusiform initial; *r.i* – ray initials

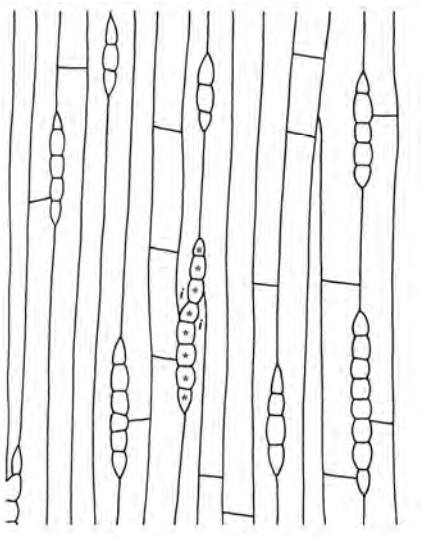

Fig. 2. **Cambium nearby wound soon after injuring, numerous transverse divisions of the fusiform initials:** *i* – intrusively elongating fusiform initials; *asterics* – strand of the ray initials passively rotated by the elongating fusiform initials

Results

Serial tangential sections of the post-wounding secondary xylem near the wound show clearly that very many fusiform cambial initials started dividing transversally soon after injuring (Fig. 2). Resulted daughter fusiform initials began elongating by means of apical intrusive growth (Fig. 3, p. 21). Elongation of these cells was oblique and caused thereof deflection of the fusiform initial orientation from the stem/root axis (Fig. 4, p. 21). The fusiform initials continued to divide transversally (Fig. 3–5, p. 21) and to elongate intrusively obliquely though the intensity of their divisions was decreasing. Very many fusiform initials were eliminated just after they had appeared. Nevertheless, the number of the fusiform initials was increasing due to their repeating transversal divisions to heel the wound.

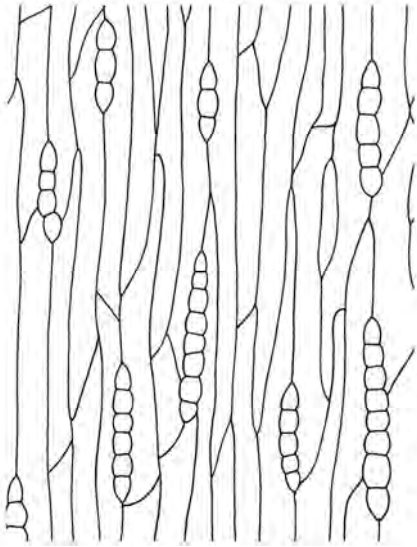

Fig. 3. **Intrusive elongation of the fusiform initials produced by the transverse divisions of their mother fusiform initials**

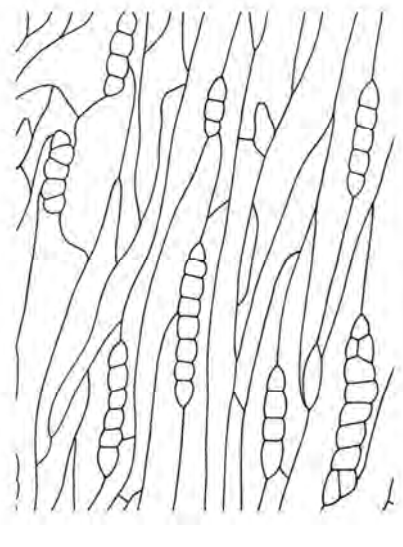

Fig. 4. **Initial deflection of the cambial initials from the stem axis**

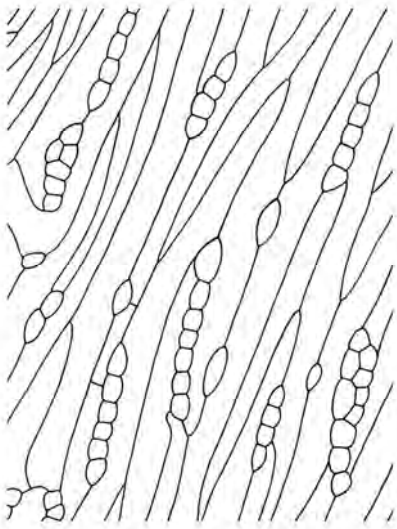

Fig. 5. **Increased deflection of the cambial initials at later moment than that shown in Fig. 4**

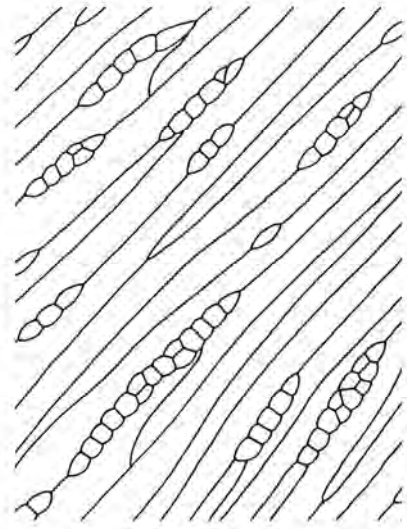

Fig. 6. **Oblique orientation of the cambial initials at the end of experiment**

Every surviving fusiform initial grew a bit obliquely in relation to orientation of its mother cell. That is why the deflection of the fusiform initials was increasing in time (Fig. 3–5, p. 21) to become about 44˚ to stem/root axis by the end of the experiment (Fig. 6, p. 21). The strands of the ray initials became similarly oblique. Accordingly, such oblique orientation was inherent in all constituents of the secondary xylem and secondary phloem which were produced by these oblique cambial initials.

Discussion and conclusions

Every fusiform initial tends to be as long as its mother one. Thereof, the new fusiform initial has to grow intrusively to approximate its mother cell length. The shorter is originally the cell, the more intensive is its elongation growth. As the transverse divisions of the fusiform initials generate the shortest ones, these divisions indirectly cause the most intensive elongation growth of arising fusiform initials. The elongation of these cells is always slightly oblique in relation to orientation of their mother cells. That is why the distinctive cambial-cell re-orientation results from the extensive oblique elongating of numerous fusiform initials. There are elongating fusiform initials that actively re-orient cells of cambium adjoining the wound. Strands of the ray initials are passively re-oriented due to intrusive growing of adjacent fusiform initials (Fig. 2, p. 20). The mode of cell re-orientation in the cambium near the wound is thus quite identical to that in the completely intact cambium as described elsewhere (Bannan, 1966; Hejnowicz, 1968; Krawczyczyn, 1971; etc). However, the scope of this post-wounding cell re-orientation is much greater. Large-scale re-orientation of the cambial initials close to destroyed cambium is certainly a consequence of intensive generating of the fusiform initials to substitute the destroyed ones and to repair the injured part of cambium.

Intensive restoring of the fusiform initial number after injuring the cambium does not demand special explanations. However, there are pseudotransverse divisions of the fusiform initials that are fit to multiply typically such cells. The two modes, viz. pseudotransverse cell divisions and real transverse ones, are likely to be equally able to generate new fusiform cambial cells. They are different in that only transverse divisions of the fusiform initials cause subsequent large-scaled elongating of the daughter fusiform initials which results in oblique re-orientation of all

cambial cells. Therefore, there is the oblique re-orientation of cambial cells nearby the destroyed cambium that is of importance for repairing injured cambium.

Functional results of re-orientation of the fusiform initials of intact cambium have been discussed elsewhere (Esau, 1953; Bannan, 1966). However, such a re-orientation is much less distinctive than that takes place in cambium adjoin wound. Then, functional results of re-orientation of intact-cambium initials and those of injuring-induced initial re-orientation are unlikely to be identical. I believe that biological significance of the oblique re-orientation of the fusiform initials of cambium under repairing is as follows.

Partial injury of the cambium primarily results in some deficiency of the secondary xylem in the trunk (Fig. 7, p. 24). Besides, the cambium situated above its destroyed part continues to produce inward the secondary xylem. The tracheids of the latter one would efficiently have conducted water if only they had contacted lower-situated counterparts to be supplied therefrom. As there are no these counterparts, the tracheids under consideration are only supplied by tangentially (= transversely) transferred water (Fig. 7 A, p. 24). Longitudinal conductivity of the secondary xylem is few hundred times as much as its transverse conductivity (Перелыгин, 1969). The tracheids just above the wound can hardly receive the water to conduct it upward efficiently. Accordingly, the wedge-shaped part of inefficiently functioning secondary xylem develops above the wound (Fig. 7 A, p. 24). This xylem part certainly diminishes the total water-conductivity of the trunk.

Multiplying fusiform initials gradually fill the ‘gap’ in the cambium. If they multiplied by means of typical pseudotransverse cell divisions, they would retain strictly longitudinal orientation. If so, they would very slowly fill the cambium ‘gap’ because of very small tangential dimensions of the cambial cells (Fig. 7 B, p. 24). Then, the xylem deficiency would not be made up for rather long period of time and total water-conductivity of the trunk would not be restored either.

Repeating transversal divisions of the fusiform initials result in their high deflection. Highly oblique fusiform initials can more rapidly fill the cambium ‘gap’ than the strictly longitudinal ones (Fig. 7 C, p. 24). Oblique fusiform initials produce identically oblique tracheids. Such tracheids maintain oblique water-current to supply directly some their counter-

parts which are produced above the wound. This water-current is noteworthy to run along the (oblique) tracheids. Longitudinal water resistance of the tracheids is few hundred times less than tangential (= transverse) one. Therefore, the tracheids produced above the wound are supplied more efficiently to make the wedge-shaped part of inefficiently conducting xylem above the wound narrower and shorter. Accordingly, the total water-conductance of the trunk more efficiently recovers.

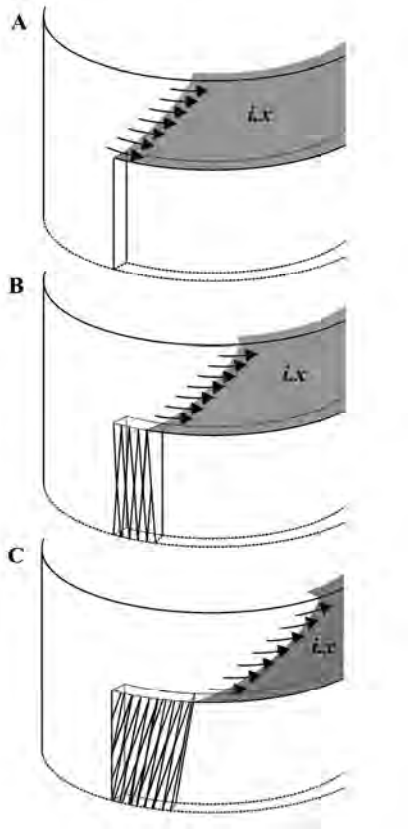

Fig. 7. **Functional results of injured cambium.**
A – without cambium reparation; B – cambium repairing by means of producing longitudinal initials; C – cambium repairing by means of producing oblique initials: *i.x* – inefficiently functioning secondary xylem; *arrows* – water flows

Intensive producing of the secondary xylem by survived cambium nearby the wound could hypothetically restore water-conductivity of the trunk without tracheid re-orientation. However, such a hypothetical process would be rather resource-consuming. If distinctive oblique re-orientation of the fusiform initials takes place, both producing secondary xylem and recovering water-conductance of the trunk are much less resource-consuming.

The same reasoning is relevant as regards recovering assimilate transport through the secondary phloem after the cambium has been injured. The only correction is to be made that the phloem transport is descending.

So, longitudinal to oblique re-orientation of the fusiform cambial cells nearby the destroyed cambium is a mode to diminish substances and energy to be used for repairing injured cambium and for restoring conductivity of the trunk. The more rapid is process of fusiform initial re-orientation, the more economical are cambium repairing and conductivity restoring. Rate of this re-orientation is specifically determined by the frequency of transversal divisions of the fusiform initials (Hejnowicz, 1968). More efficient repairing of the injured cambium is consequently a biological significance of the repeating transverse divisions of the fusiform initials nearby destroyed part of cambium.

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