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Peculiarities of parenchyma inclusions in the decorative wood of Karelian birch, burls and gnarls

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Summary: The origin of parenchyma inclusions in the wood of Karelian birch, burls and gnarls is considered here. It is shown that parenchyma congestions in the typical decorative wood of Karelian birch and burl wood have different origins. The wood of gnarls usually has no parenchymal formations, however, but sometimes parenchyma of overgrown tunnels caused by larvae of the fly *Phytobia* spp. can be found there, just as in the wood of Karelian birch and burls.

Keywords: Karelian birch, burls, gnarls, patterned wood, parenchyma congestions

Excrescences of various forms, sizes and locations can be seen on the trunks of many woody plants. Although the reasons of their formation are different, they have much in common on macro and/ or micro level due to the increase proportion of parenchymal cells in the wood (KOROVIN et al. 2003). Inclusions of parenchyma are the cause of disturbance in orientation of wood vessels and fibers. All together these structure features impart a decorative look to the wood. Decorative wood of Karelian birch (*Betula pendula* Roth var. *carelica* (Merckl.) Hämet-Ahti), burls and gnarls of the common silver birch (*B. pendula* var. *pendula*) and downy birch (*B. pubescens* Ehrh.) are well known in the world. At the same time they are often confused which each other (ZABOROVSKI 1932; NEISHTADT 1948; LAVROV 1955). Causes of appearance and the structural features of parenchyma inclusions in the wood of these three taxa are considered in the present article.

Materials and methods

Samples of the Karelian birch wood (*Betula pendula* var. *carelica*) and the wood of burls and gnarls from the common silver birch (*B. pendula* var. *pendula*) and downy birch (*B. pubescens*) were collected in the forests of the Republic of Karelia, Pskov, Leningrad and Moscow oblast (Russia) in 2007–2014.

Wood macrostructure. Cuts of the wood were polished and varnished to highlight the wood texture.

Wood microstructure. Blocks of wood 3 mm^3 in size were cut out. The samples were fixed by following a standard technique in 30 g/l glutaraldehyde, 25 g/l sucrose, 0.1 M phosphate buffer (pH 7.4) at room temperature for 6 h. After the samples had been rinsed in buffer, post-fixation was carried out in $20 \text{ g/l} \text{ OsO}_4$ and 0.1 M phosphate buffer (pH 8.0) at 6°C for 13 h. Then, the material was washed in distilled water, dehydrated by an ascending ethanol series and embedded in epoxy resin. Sections were cut with a LKB-Ultratome IV (LKB, Sweden) using glass knives, stained with safranin and examined and photographed under the light microscope AxioImager A1 (Carl Zeiss, Germany).

N. N. NIKOLAEVA, L. L. NOVITSKAYA & F. V. KUSHNIR



Peculiarities of parenchyma inclusions in the decorative wood of Karelian birch

Results and discussion

Parenchyma in wood consists of poorly differentiated live cells whose main function is storage of substances. Usually the radially oriented ray parenchyma and the axial parenchyma, which forms an extensive network of vertically oriented strands, can be distinguished in wood. In addition, there are large abnormal accumulations of parenchyma in the patterned wood of Karelian birch (Fig. 1A). On cross sections they look like V-shaped inclusions or dots, dashes or commas (Fig. 1B, C). According to results of our research, changes in the pattern of the trunk tissue differentiation in Karelian birch are due to an excess of sucrose in the local areas of the conducting phloem and cambium zone (NOVITSKAYA 1998, 1999, 2008; NOVITSKAYA & KUSHNIR 2006). The morphogenetic effect of sucrose is due to the impact of its stream on sugar sensitive proteins of cell membranes. Changes in their functional state affect the expression of genes (GRAHAM 1996; KOCH 1996; SMEEKENS 1998; SHEEN et al. 1999; GIBSON 2000, 2004). Due to an excess of sucrose in birch trunk, the cambium derivatives turn into parenchyma cells instead of differentiating into vessels and fibers. In zones with abnormal parenchyma accumulation deflections of the annual ring arise causing the syndrome of stem pitting (Fig. 1B).

There is one more type of parenchyma in the wood of Karelian birch: pith-ray flecks or medullary spots (Fig. 1D, E). They represent the tunnels grubbed by larvae of the fly *Phytobia* spp. (PERELYGIN 1957), filled with parenchymal cells (Fig. 1D–H). Larvae move between bark and wood and eat juicy cell layers of the cambial zone. Cells of radial rays extending into the cavity of the larval tunnel take active part in the processes of regeneration. Cells of the rays increase in size and divide intensively. As a result, almost all rays in front of the tunnels become wider (Fig. 1G). Subsequent proliferation of ray cells leads to a filling of the cavity with parenchyma cells. Axial parenchyma cells also participate in regeneration. Under the action of wound metabolites or substances secreted by insects these cells as well as ray cells dedifferentiate and gain the ability to divide (NOVITSKAYA 1998; KOROVIN et al. 2003). After filling the wound cavity with parenchyma cells, the integrity of the cambium is restored and damaged areas plunge gradually into new wood layers. Normalization of wood structure does not occur immediately and is accompanied by a gradual narrowing of radial rays to their normal width. On cross sections, overgrown larval tunnels appear like multiple medullae because of the change of the ray width on 'entrance' and 'exit' of the abnormal zone (Fig. 1G).

The patterned wood of Karelian birch (Fig. 1A, B) is often confused with burl wood (Fig. 2E, F) probably due to similarities at first glance. They both have pearlescent shine on their polished surface due to irregular grain (disturbance of the vertical orientation) of vessels and fibers, dark-colored inclusions which represent clusters of parenchyma cells and formations on the tree trunk resembling excrescences (Fig. 2A).

Burl is an excrescence of various forms on branches, stems and roots (Fig. 2C, D), which has been formed as a result of increased cambium activity caused by the growth of dormant and

Figure 1. Karelian birch (*Betula pendula* var. *carelica*). A – tangential section of wood; B–E, G – cross section of wood; C – cross-section in the zone of an abnormal parenchyma congestion which forms the characteristic wood texture; D – combination of typical texture of the Karelian birch wood and larval tunnels in the dash form of various sizes filled with wound parenchyma; E – fragment of D; F – larva of *Phytobia* spp.; G – white arrows indicate two larval tunnels filled with parenchyma tissue in a zone of the last annual ring; H – network of larva tunnels on the trunk surface. Scale bars A = 5 cm; B, D, H = 1 cm; C, G = 500 µm; E, F = 0.5 cm.

N. N. NIKOLAEVA, L. L. NOVITSKAYA & F. V. KUSHNIR



Figure 2. A – Karelian birch tree; B – surface of the Karelian birch debarked trunk; C – burl on the birch trunk; D – surface of debarked burls; E – tangential section of a burl with dark inclusions of parenchymal bud traces in the form of eye-like markings surrounded by swirls of distorted wood; F – cross section of burl where the waviness of wood surrounding bud traces is well visible, arrows indicate larva tunnels filled by wound parenchyma; G – radial section of burl with larva traces (black arrows); 'eye-like markings' surrounded by swirls of distorted wood tissues (black circle) can be seen and by the way one of the buds from the area of bud initiation until its exit to the surface (white arrow). Scale bars B, C = 5 cm; D = 10 cm; E–G = 1 cm.

Peculiarities of parenchyma inclusions in the decorative wood of Karelian birch

adventitious buds. Due to the growth of a large number of bud axes, the surface of the burl has numerous outgrowths similar to thorns under the bark (Fig. 2D).

Dark parenchyma inclusions of bud traces and the nacreous gloss of tissues surrounding them are responsible for decorative qualities of burl wood (Fig. 2E). The local zone around the bud trace consists of xylem elements that have lost their vertical position. Light reflects from the walls of fibers disposed at different angles to the cutting plane giving a nacreous gloss to the wood. The remaining wood mass of the excrescence can consist of xylem elements having the usual orientation. Saturation of the wood pattern in a burl may vary depending on the number of bud traces in a unique area of a cut.

If the plane of a cut is perpendicular to the trunk axis (transverse section) and parallel to the general direction of the burl bud growth, strands of the sheath bud traces in the form of rays diverging from the center and resembling flames will be visible (Fig. 2F). It is difficult to follow the strand of the bud trace parenchyma in the transverse section, because the direction of bud growth can vary and does not coincide with the plane of a cut. Bud trace tortuosity is the reason that on a radial burl cut (referring to the trunk axis) traces of the buds in the form of 'eye-like markings' surrounded by abnormal wood and strands of parenchyma extending from the center of trunk almost up to the bud exit on the surface can be seen (Fig. 2G).

Burl is sometimes confused with gnarl which is a spherical or another formed outgrowth on a tree trunk (Fig. 3A). Gnarl formation is caused by enhanced cambium activity but no way associated to the development of buds and any precisely established pathogen of abnormal changes in the stem structure (KOROVIN et al. 2003). Unlike burl, the gnarl is formed almost exclusively on the trunk, rarely on the branches of a tree. Wood of gnarl just like wood of burl has wavy fibrous elements that create the effect of a pearlescent sheen on the polished surface of the tangential cut (referring to the trunk axis) (Fig. 3D–G). Some of the axial anatomical elements have a differently directed orientation (= wavy grain). Sometimes wavy grain cannot be seen, but sometimes it creates a 3-D effect (Fig. 3C–G).

The wood surface of gnarl under the bark is usually smooth (Fig. 3B) unlike the wood of Karelian birch and burl. However, sometimes there are gnarls in peripheral zones where a quite deep ingrowth of bark tissues of varying intensity can be seen (Fig. 3D–E). In this case, the surface of debarked gnarl is bumpy. It is caused by the existence of activation and inhibition centers of the cambium activity.

Unlike the wood of burl and Karelian birch, a typical wood of gnarl has no parenchyma inclusions. In this connection it is interesting to analyze the sample of gnarl whose tangential cut (referring to the trunk axis) has a well pronounced serrated pattern (Fig. 3G). A detailed study showed that the dark inclusions of parenchyma tissue are overgrown larval tunnels similar to those observed in the wood of Karelian birch and burls (Figs 1D; 2F–G). If the direction of a larval tunnel coincides with the plane of the cut, the tunnels look like lines of different lengths. If the cut extends along the external or internal edge of overgrown tunnels in the zone of abnormal expansion of radial rays (Fig. 1G), a broken line with sharp contours can be seen on the surface of a tangential cut (Fig. 3G–H). Large annual wood increments indicate that a gnarl on a tree trunk can be considered as attracting center for a significant flow of assimilates. High density of larval tunnels may cause abundance of nutrients.

Thus, parenchyma inclusions in the wood of Karelian birch, burls and gnarls have different origins. In Karelian birch they appear as a result of disturbances of cambium derivative differentiation in connection with the appearance of an excess of assimilates in trunk tissues. In the wood of burls



Figure 3. Gnarls of *B. pendula* and *B. pubescens*. A – gnarl on the trunk; B – smooth surface of debarked gnarl; C – longitudinal section of a gnarl; D – gnarl with a few bark tissue inclusions; E – gnarl with lots of bark tissue inclusions; F – polished tangential section of a gnarl with obvious 3-D effect; G – gnarl with numerous larval traces; H – fragment of G. Scale bars B–G = 5 cm; H = 1 cm.

Peculiarities of parenchyma inclusions in the decorative wood of Karelian birch

parenchyma inclusions represent traces of buds. In both types parenchymal formations are often supplemented by parenchyma of overgrown larval tunnels. Usually the wood of gnarls does not contain decorative inclusions of parenchyma, but sometimes it is possible to find abundant larval tunnels and/or inclusions of bark tissues. Disorientation of vessels and fibers imparting a nacreous gloss and a visual effect of a rough surface of the polished wood cuts is a common feature of all investigated wood types.

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N. N. NIKOLAEVA, L. L. NOVITSKAYA & F. V. KUSHNIR

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