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Endogenous variability of the figured wood of Karelian birch

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Summary: Karelian birch (*Betula pendula* Roth var. *carelica* (Mercl.) Hämet-Ahti) is highly diverse in terms of the location and density of wood figure in trunk sections. We have previously showed that figured wood development in this tree may be induced by excessive content of sucrose in trunk tissues. Relying on our assumption of the regulatory role of sucrose in the formation of figured wood in Karelian birch, we managed to provide a scientific explanation to structural peculiarities of figured wood, different density of the figure, various localizations of figured wood in a trunk, pulsed development of the wood structural abnormalities, relationship between the trunk radial growth rate, bark thickness and wood texture. It is for the first time that they appear as an outcome of sucrose excess in the trunk rather than just as scattered facts.

Keywords: *Betula pendula* Roth var. *carelica*, sucrose excess, wood structure, density and localization of wood figure, wood anatomy

The figured wood of Karelian birch (*Betula pendula* var. *carelica*) resembles marble in pattern and is rightfully regarded one of the most decorative woods in the world (Fig. 1). It is also known as curly birch, Masur birch, Karelische Maserbirke, Visakoivu or Masurbjörk (Ahlsved et al. 1979).

A comparative study of anatomical, cytological and biochemical features of the trunk in Karelian birch and silver birch (*B. pendula* var. *pendula*) has led us to the conclusion that figured wood forms due to excess of sucrose in the conducting phloem and cambial zone (Novitskaya 1997, 2008; Novitskaya & Kushnir 2006; Galibina et al. 2015a, b). Being the principal form for assimilate transport, sucrose plays a special role in the life of a plant. Sucrose synthesized in green leaves is exported via the phloem to supply sink tissues with energy and carbon resources. Soluble sugars such as sucrose and glucose have been recognized as key signaling molecules which regulate a variety of genes and can affect cell division, growth, differentiation, metabolism and resource allocation in plants (Koch 1996; Lalonde 1999; Sheen et al. 1999; Yu 1999; Gibson 2000, 2004; Smeekens 2000; Rolland et al. 2002). As a consequence, a change in sucrose concentration in the cambial zone of a woody plant would influence the direction of the metabolism of cambial derivatives and, hence, may alter the programme of xylem and phloem cell differentiation.

We know that proof for any hypothesis is gained by explaining diverse, often scattered facts, which had previously been unclear. The latter is very true for the biological characteristics of Karelian birch. In this paper, we consider examples of endogenous variability of the figured wood in Karelian birch trunks from the viewpoint of sucrose supply to trunk tissues.

Materials and methods

The study objects were trees of Karelian birch (*Betula pendula* Roth var. *carelica* (Mercl.) Hämet-Ahti) and silver birch (*B. pendula* var. *pendula*) growing in planted stands in the Republic of

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Karelia. The plants were raised from seeds obtained by control-pollination. The age of the plants was 20 to 50 years. Plant material was collected during 2007–2016.

Wood microstructure. Wood samples were taken from silver birch trees and Karelian birch trees (3 trees of each form). Trees were aged 25 years. Cubes (side length 3 mm) were cut from outer layers of wood approximately at 1.3 m above the ground. In Karelian birch, samples were taken from areas with high density of figure.

The material was fixed following the technique used in electron microscopy (Hunter 1993). Samples were fixed in 3% glutaraldehyde : 0.1 M sucrose : 0.1 M phosphate buffer (pH 7.4) at room temperature for 6 h. After rinsing in buffer, postfixation was carried out in 2% OsO_4 : 0.1 M phosphate buffer (pH 8.0) at 6°C for 13 h. After washing in distilled water, the material was dehydrated in an ethanol series (30%, 50%, 70%, 85%, 96%, 100%) and embedded in epoxy resin. Cross and tangential sections (square 3 × 3 mm, 2 µm thick) were cut on an LKB-Ultratome IV (Sweden), using glass knives.

Sections were stained with 1% aqueous safranin, which is a general stain for lignified cell walls of the wood (Srebotnik & Messner 1994). The second stain used was OsO_4, which works as a stain as well as a fixative. Osmium tetroxide reacts with fatty acids of cell membranes (Thiéry et al. 1995) and with phenols, such as tannin in vacuoles (Shnawa et al. 2011). Vacuoles of parenchyma cells in Karelian birch trunk tissues contain very high amounts of tannins, which are detected any time around the year (Barilskaya 1978; Novitskaya & Kushnir 2006). Reduction of Os produces dark brown color in processed tissue (Kuwajima 2011). That is why osmium stained parenchyma cells in birch wood stand out distinctly from the other xylem elements (Barilskaya 1978; Novitskaya & Kushnir 2006).

Stained sections were mounted in Canada balm and examined with an AxioImager A1 light microscope (Carl Zeiss, Germany) equipped with a ProgRess C10^{plus} camera (Jenoptic, Germany) at 100× magnification.

Wood macrostructure. The richness of figure in Karelian birch was preliminarily estimated using the technique suggested by Yermakov (1986). The technique is based on the known correlation between the intensity of figure in Karelian birch wood and the number of pits (depressions) on the wood surface exposed by debarking. A rectangular piece of bark 3 × 4 cm, with the longer side oriented along the trunk, was cut out with a grafting knife in the period of high cambial activity, when the bark can be easily separated from wood. After the bark had been removed, the number of pits in the exposed zone was quickly counted, and then recalculated per 1 cm^2. Figure was considered very dense, when there were 7 or more depressions per 1 cm^2 (d.f. – densely figured wood), moderately dense with 4–6 depressions (m.f. – medium figured wood), sparse with 1–3 pits (w.f. – weakly figured wood). The removed bark was then inserted back in the gap and fixed in place by adhesive tape wrapped around the trunk. Two or three weeks later, bark and wood tissues regrew together. This technique was applied to over 80 trees, 22 of which were sampled and sawn down to demonstrate various types of wood figure and to study the parameters of wood macrostructure. Three silver birch trees were taken for a comparison.

Wood macrostructure was examined for the following characteristics: (i) wood texture variations, (ii) correlations between wood texture and habitat conditions and (iii) width of annual rings and bark thickness in figured and non-figured wood zones.

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Transverse sections (3 cm thick) were sawn from the tree trunks at 1.0–1.5 m above the ground. One section was taken from one tree. As a result, 22 sawn sections were thus made for the study. In the paper, various types of figured wood formation are illustrated by 12 Karelian birch trees. The sawn surfaces were polished and varnished to highlight the texture and then photographed.

Influence of light on figured wood formation is shown on cross-sections of trees growing in (i) a high density stand with trees arranged in a 2 × 2 m grid (3 trees), (ii) at the boundary of this stand and a field (3 trees) and (iii) plots thinned 6 and 15 years ago (4 trees).

The width of annual rings was measured in samples with straight-grained wood covering figured wood (3 trees) and vice versa (3 trees) and in the case of asymmetric formation of figured wood (on one side of the trunk) (3 trees). The measurements followed linear transects running along the radius across segments with figured and non-figured wood. Five transects across each type of wood texture were drawn per sample.

Bark thickness was measured: (i) within one sawn section opposite figured and non-figured wood segments (3 measurements in each type of texture; 3 trees) and (ii) in sawn sections demonstrating different degrees of figure intensity (w.f., m.f., d.f., strait grain – 3 trees for each type, 4 measurements were taken from the ends of two perpendicular lines running across the pith of the section). Linear dimensions of the width of annual rings and bark thickness were determined from the photographs of the polished and highlighted sawn sections using Morphology 5.0 software (Videotest, Russia).

Statistical Treatment. The data were statistically processed using the Statgraphics software package for Windows 7.0. Measurements are presented as mean values and confidence intervals. The indicated confidence intervals for all values meet 95% reliability according to Student's *t*-distribution.

Results

Wood microstructure. Silver birch has straight-grained wood (Fig. 2 A, B) with inexplicit texture (Fig. 1 A). The wood of silver birch comprises fibrous elements, vessels and parenchyma cells. Fibrous elements and vessels are clearly vertically oriented, and parenchyma cells form radial rays and vertical parenchyma strands.

Karelian birch wood is made up of the same structural elements as the wood of silver birch. Decorative qualities of Karelian birch wood arise from a combination of pearly luster and dark-coloured inclusions of various shapes (Fig. 1 B–F). The dark inclusions generating the figure are assemblages or layers of parenchymal storage tissue cells (Fig. 2 C, D). The pearly luster of the wood is due to the broken vertical strand orientation (swirling pattern) of its elements (Fig. 2 D).

Wood texture. One can see from trunk cross-sections (Figs 1; 3) that Karelian birch is highly diverse in terms of wood figure intensity and the distribution of non-figured and figured wood areas across the trunk. Structural abnormalities may begin forming in the wood at different ages of the plant and may grow either stronger or weaker or even return to normal structure formation.

Wood texture and light conditions in the habitat. A vivid example of how light influences figured wood formation is the asymmetric wood texture in Karelian birch growing at the boundary of high density stand and a field. Figured wood in such plants forms on the light-exposed side of the crown (Fig. 3 A–C).

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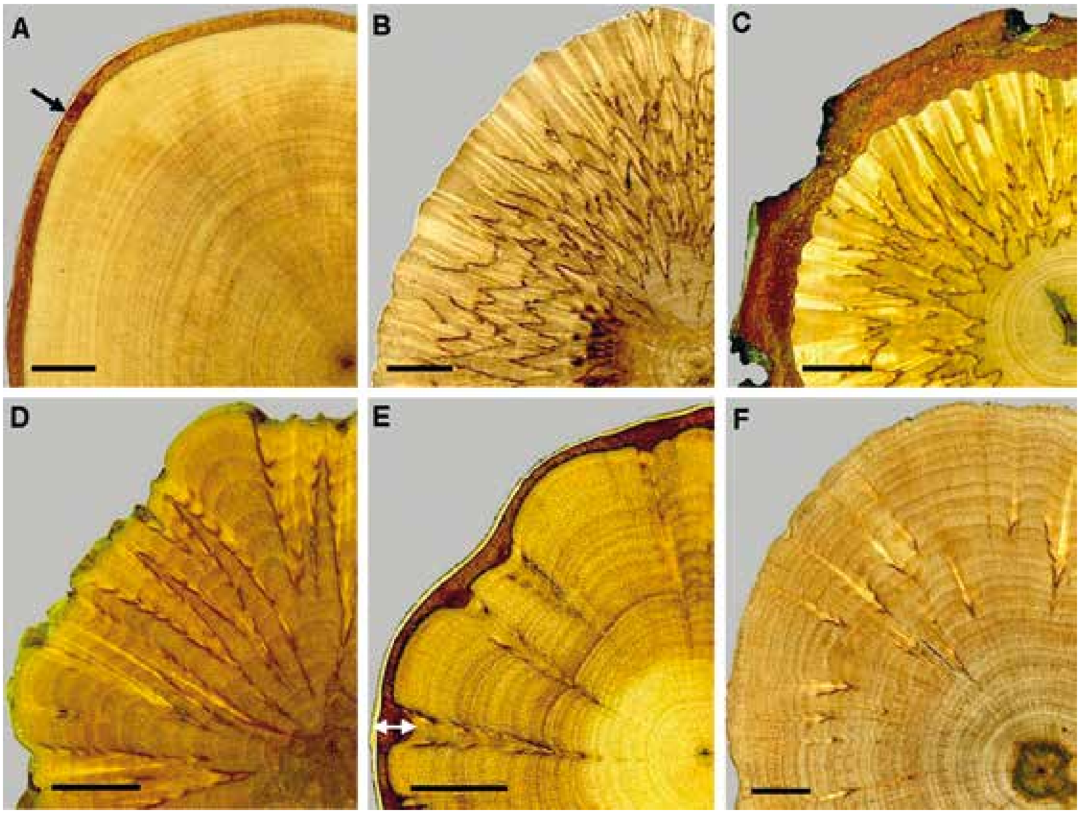

Figure 1. Cross-sections of *Betula pendula* Roth trunks. A – Plain texture of silver birch (*B. pendula* var. *pendula)*. B–F – Karelian birch (*B. pendula* var. *carelica*) wood texture with different degrees of richness. B – Densely figured wood (d.f.); C, D – Medium figured wood (m.f.); E, F – Weakly figured wood (w.f.). A, C, E – With bark, arrows point on bark; B, D, F – Without bark. Scale bars = 1 cm.

Karelian birch trees in high density stand gradually fall under shade of neighboring trees. Reduced light results in non-figured wood forming around figured wood (Fig. 3 D, E). Thinnings launch the opposite process – straight-grained wood gets overgrown by figured wood (Fig. 3 F, G).

Wood texture and the trunk radial growth rate. Rich figure forms as annual wood increment is enlarged (Figs 3; 4). A good example of such correlation is the formation of figured grain in an eccentric Karelian birch trunk, where annual rings in the curly wood area are nearly 3 times wider than in the rest of the trunk cross-section (Fig. 3 A–C). The widening of annual rings is obvious at the transition from normal or relatively normal growth to figured wood formation (Fig. 3 F, G).

Wood texture and bark thickness. An important distinctive feature of Karelian birch is its bark, which is several times thicker than in silver birch (Figs 1 A, C, E; 3 A, H, I). Correlation between bark thickness and wood texture may be clearly visible within a single cross-section: bark in front of the sectors with figured wood is much thicker than at adjacent straight-grained areas (Figs 1 E; 3 A; 5).

Pulsed development of structural abnormalities in Karelian birch wood. In spring, during cambial reactivation, the development of dark inclusions in Karelian birch wood usually gets interrupted (Fig. 3 I). The cambium begins to deposit xylem layers with a relatively normal structure, mainly consisting of fibrous elements and vessels. However, after some time massive differentiation of

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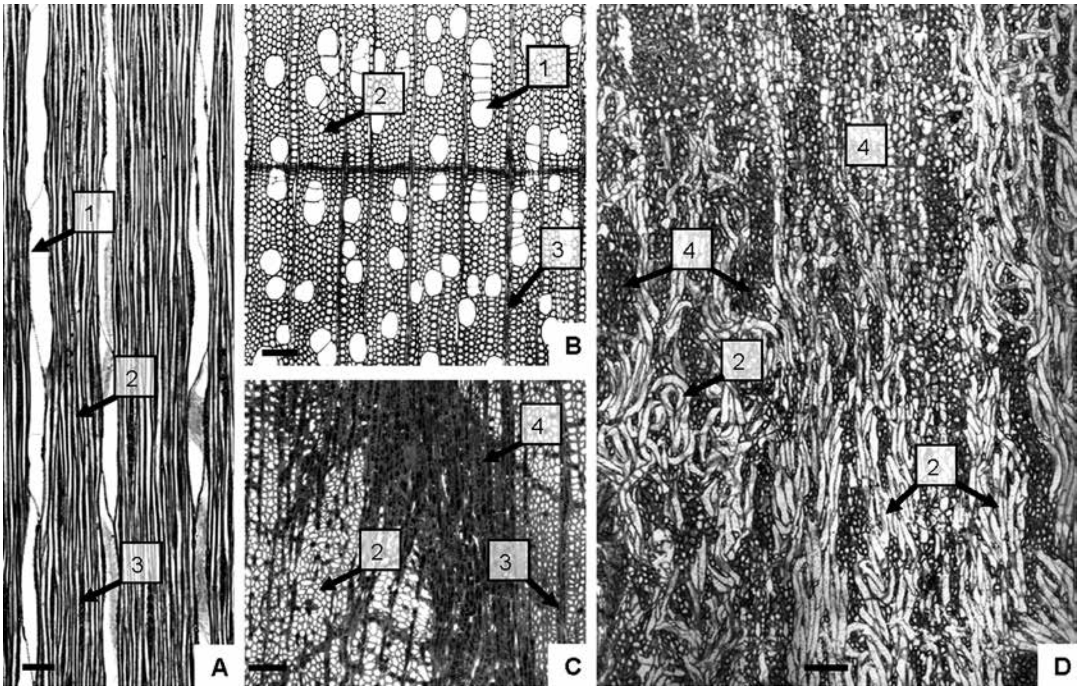

Figure 2. Sections of the wood of silver birch (A, B) and Karelian birch (C, D). B, C – Cross-sections; A, D – Tangential sections. 1 – vessels, 2 – fibrous tracheids, 3 – ray parenchyma, 4 – abnormal aggregations of parenchyma. Scale bars = 100 µm.

parenchyma cells resumes. In some cases this phenomenon is explicit (Fig. 3 I–K), while in other cases layers of 'normal' wood are very thin and dark parenchyma inclusions look continuous.

Discussion

Histological composition of *Betula pendula* wood. Information about the histological composition of the wood of *Betula pendula* in literature is contradictory. Some authors declare that water-conducting elements of the birch wood are vessels, whereas mechanical elements are fibres, but do not specify the type of the fibres (Luostarinen & Verkasalo 2000; Heräjärvi 2005; Koch & Schmitt 2013), others speak of vessels and tracheids (Kedrov 2012), yet others believe that fibrous elements in birch wood represent a form transitional between tracheids and libriform fibres, i.e. they are fibrous tracheids (Barilskaya 1978; Baum 2001; Schwarze 2007; Price & Macdonald 2012).

The traits of tracheids in the fibrous elements of *Betula pendula* are moderately thickened (up to 3 µm) cell walls, bordered pits inside them and pores confined to radial walls (Barilskaya 1978). The walls of libriform fibres are usually thicker and have small, slit-like or dot-like pits, which are scattered over the fibre wall (Ilvessalo-Pfaffli 1995). At the same time, bordered pits in the walls of fibrous elements in silver birch are very scattered, most of them with slit-like inner openings. This suggests that fibrous elements are very fit for the mechanical support function and are structurally similar to libriform fibres (Barilskaya 1978).

The presence of libriform fibres in wood is known to be closely correlated with storeyed cambium and axial parenchyma of the paratracheal type (Kedrov 2012). Indicators of the absence of typical

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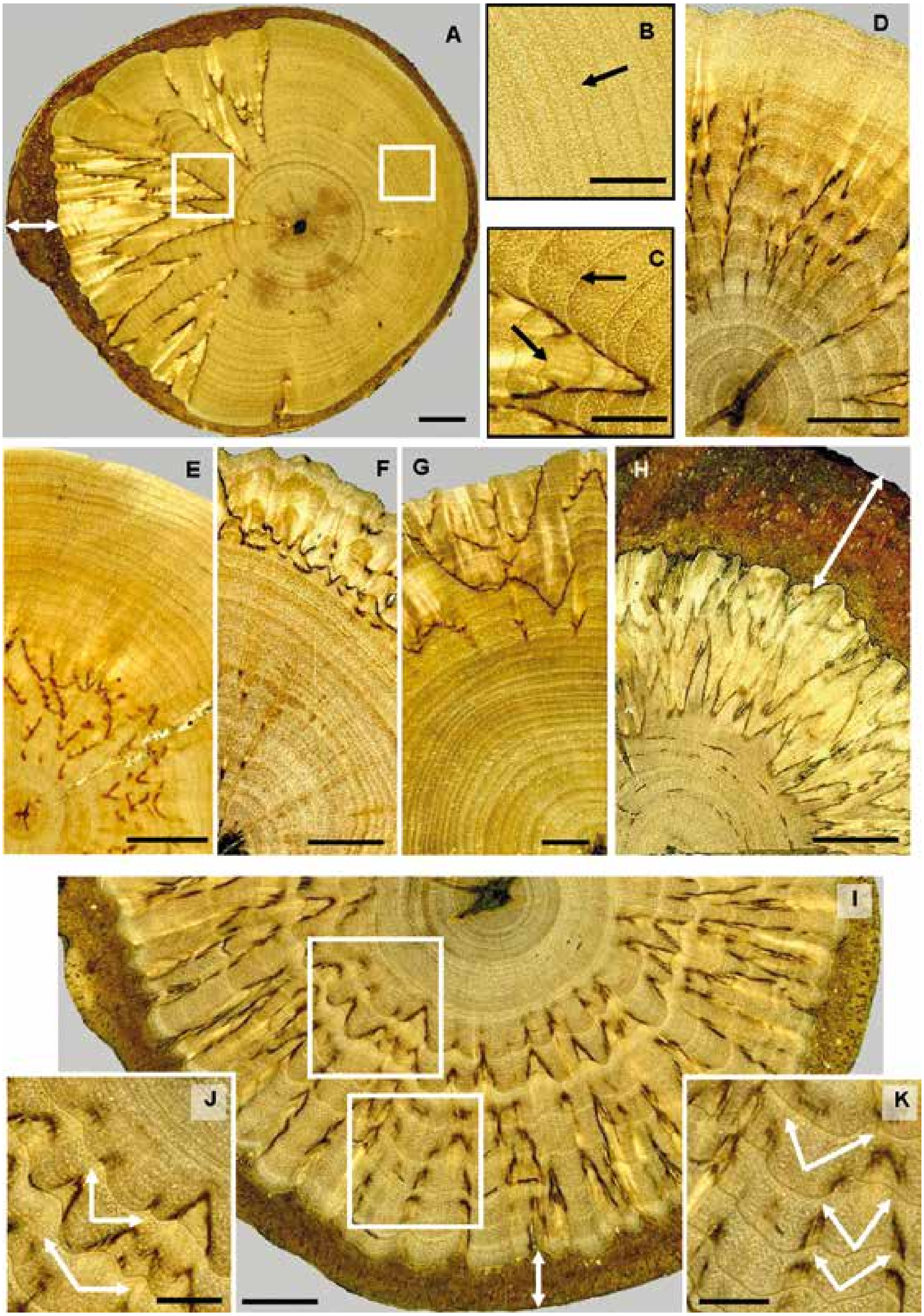

Figure 3. Cross-sections of Karelian birch wood. A – Asymmetric distribution of figure in a cross-section of a trunk of a tree growing at the boundary of a high density stand and a field; figured wood is situated on the light-exposed side of the crown; double arrow points to thicker bark on the figured wood side. Scale bar = 1 cm. B, C – Details of Fig. 3 A demonstrating variations in the width of annual rings in non-figured / figured wood areas (arrows point to the ▶

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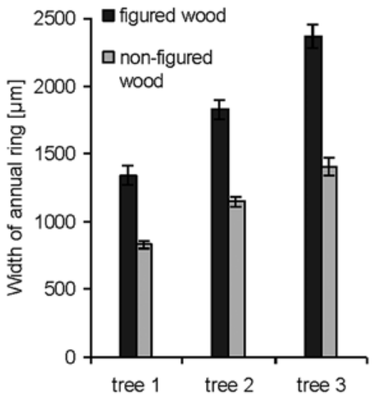

Figure 4. Average width of annual ring in Karelian birch trees in zones with figured and non-figured wood within a single cross-section.

libriform fibres in *Betula pendula* wood are its non-storeyed arrangement of cambial cells and apotracheal parenchyma (Barilskaya 1978). Another indicator of the transitional type of fibrous elements in the birch wood is the specific characteristic of the monomeric composition of lignin within cell walls. It has been shown for many species that vessel and tracheid cell walls contain high amounts of guaiacyl lignin, and the cell walls of libriform fibres have high concentrations of syringyl lignin (Schwarze et al. 2000; Baum 2001). When subjected to UV microscopy, vessels in silver birch wood were stained typical for high levels of guaiacyl lignin, and the bulk of the wood was made up of elements with very low syringyl lignin concentrations (Baum 2001).

Summarizing these data we came to the conclusion that fibrous elements in *Betula pendula* wood are represented by fibrous tracheids.

Structural peculiarities of Karelian birch wood and sucrose level. The dark lines creating the figure in Karelian birch wood (Figs 1 B–F; 3) are aggregations of parenchyma cells (Fig. 2 C, D). There are data demonstrating the percentages of structural elements in silver birch (*B. pendula* var. *pendula*) wood and in Karelian birch wood: silver birch has fibrous tracheids (62.6%), vessels (23.7%) and parenchyma cells (13.7%); Karelian birch (with dense figure) has fibrous tracheids (21.1%), vessels (1.9%) and parenchyma (77%) (Lyubavskaya 1978). Thus, parenchyma cells in figured Karelian birch wood are more numerous.

The influence of light (Fig. 3 A–G) and the stage in the growing season (Fig. 3 I) on the formation of figured wood in Karelian birch proves that abnormal xylogenesis in this case is determined not only by genetic factors, but also depends on the environmental conditions and physiological state of the tree.

Opinions have been expressed that development of structural abnormalities in Karelian birch trunk is associated with changes in their metabolic status. There are currently two hypotheses

► annual ring boundary). Scale bar = 0.5 cm. D, E – Plain wood forming around figured wood in Karelian birch plants shaded by surrounding trees. Scale bar = 1 cm. F, G – Plain wood getting surrounded by figured wood in trees left in the stand after thinning. Scale bar = 1 cm. H – Very thick bark formed in the zone of densely figured wood. Scale bar = 1 cm. I – Pulsed pattern in abnormal wood development; double arrow indicates bark thickness. Scale bar = 1 cm. J, K – Details of Fig. 3 I; arrows indicate wood layers without parenchyma inclusions annually formed at the beginning of cambium activity. Scale bar = 0.5 cm.

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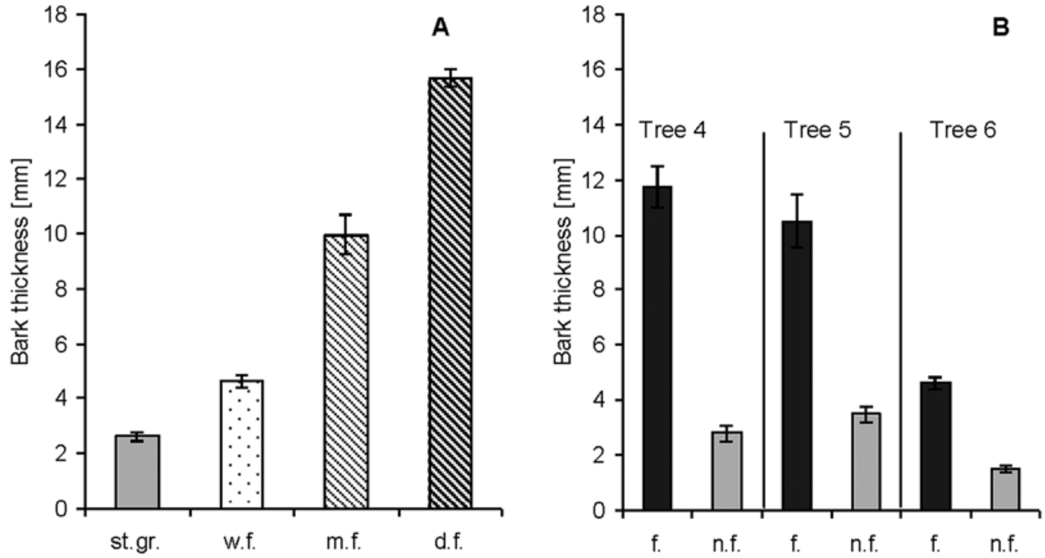

Figure 5. Bark thickness in cross-sections of silver birch and Karelian birch. A – Thickness of bark in cross-sections with different degrees of figured wood richness (abbreviations as in Fig. 1); B – Thickness of bark within a single cross-section in front of the sectors with figured (f.) and non-figured (n.f.) wood.

concerning the metabolic causes of abnormal cambial growth induction in Karelian birch. Some authors attribute this phenomenon mainly to a rise in the auxin level in trunk tissues (Kosichenko & Shchetinkin 1982; Shchetinkin 1987). We believe that the key role here belongs to a rise in sucrose level (Novitskaya 1997, 2008; Novitskaya & Kushnir 2006; Galibina et al. 2015b).

Auxin is needed for differentiation of vessels and tracheids (Aloni 2015). It is known that auxin is involved in plant developmental processes in the form of free hormone; the regulation of auxin action in a plant includes its reversible transition to the bound (inactive) state (Ludwig-Müller 2011).

Supporters of the 'hormonal' hypothesis of figured wood formation refer to the higher (1.8-fold) auxin content in the bark of the Karelian birch trunk as compared to silver birch (Shchetinkin 1987). It has to be stressed, however, that the bulk of IAA in silver birch is free IAA (free / bound = 2.9) and in Karelian birch it is bound IAA (free / bound = 0.5). Furthermore, areas where dense figured pattern was formed contained 4 times more bound IAA than areas with poor figured pattern within the same Karelian birch trunk (Shchetinkin 1987).

The reduced number of vessels and fibrous tracheids in the figured wood of Karelian birch indicates a decline in the content of free auxin in the xylem differentiation zone. On the other hand, these data correlate with the high level of bound auxin in tissues. Auxin is effectively bound in the plant through conjugation with glucose (IAA-glucose as the product) (Michalczuk & Bandurski 1982).

During cambial growth transport sugars in *Betula pendula* Roth phloem are nearly exclusively represented by sucrose (Novitskaya et al. 2015). Previously obtained data have led us to the conclusion that the formation of figured wood in Karelian birch is associated with excess of sucrose in the phloem (Novitskaya 1997, 2008; Novitskaya & Kushnir 2006; Galibina et al.

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2015a, b). By 'excessive' we mean the sucrose that is not utilized for cambial growth. It is known that 'excessive' sucrose is utilized in the phloem through the synthesis of storage substances (Kursanov 1984; Evert 1990; Gamalei 2004). We found that in the period of high cambial activity the conducting phloem of Karelian birch, unlike silver birch, stored high amounts of starch, lipids and tannins (Novitskaya & Kushnir 2006). These compounds are synthesized as a result of intensive utilization of sucrose: the activity of sucrose-degrading enzymes in Karelian birch phloem is 2.5 times higher than that of silver birch (Galibina et al. 2015a, b). Judging by these data, the sucrose level in Karelian birch phloem is much higher than in silver birch. In this sense, we point to papers showing that a rise in sucrose level induces storage metabolism and differentiation of storage parenchyma cells (Kursanov 1984; Simko 1994; Xu et al. 1998; Wobus & Weber 1999; Borisjuk et al. 2002, 2003).

In both birches, sucrose in phloem is cleaved by invertase (Galibina et al. 2015b), and hence, the products are glucose and fructose. In both cases the main enzyme (some 70% of total activity) is apoplastic invertase. The activity of apoplastic invertase in Karelian birch is 2.4 × higher than in silver birch (Galibina et al. 2015b). This shows evidently a higher level of glucose in Karelian birch phloem. We believe that high glucose levels promote auxin conjugation in the phloem and in the adjoining cambial zone as well, where the course of development of cambial derivatives is determined. Inactivation of auxin halts the differentiation of vessels and fibrous tracheids. In this context, elevated sucrose level induces the formation of parenchyma cells. Their clusters give a distinct pattern to the wood of Karelian birch.

Another feature of the figured wood in Karelian birch is the disrupted spatial orientation of its elongated elements (fibres, vessels) (Fig. 2 D). The result of that is grain swirl. The proper (vertical) orientation of elongated wood elements (Fig. 2 A) is caused by the growth of cells in the basipetal direction, which in turn depends on polar auxin transport. Directional auxin efflux from the cell is provided by auxin transport efflux carriers, PIN proteins (Bennet et al. 1998). During normal development of vessel elements and wood fibres, PIN proteins are accumulated on plasmalemma at the basal end of the cell, channeling polar auxin transport. The model object for studying auxin transport and the related morphogenetic effects is root growth in seedlings. It has recently been demonstrated for *Arabidopsis thaliana* that glucose controls root growth direction (Singh et al. 2014). Increasing Glc concentration not only induced root deviation from vertical, but also altered root waving and coiling. It is important that such root reaction is specific for glucose and sucrose, suggesting that osmotic changes in the medium are not solely responsible for the observed response. The mechanism of glucose action in this case is thought to be related to the fact that it can alter the expression pattern of PIN proteins in terms of its greater accumulation in a lateral cell wall (Mishra et al. 2009). As a consequence, the direction of cell growth changes, causing roots to curve.

Proceeding from the data above, we can assume that the high concentration of sucrose in trunk tissues in Karelian birch induces storage metabolism and differentiation of parenchyma cells. The elevated level of glucose resulting from sucrose cleavage promotes auxin conjugation, thus blocking the differentiation of vessels and fibrous tracheids on the one hand and leads to a disruption of the ordered orientation of the wood structural elements

Different degrees of figure density in the wood and sucrose level. Earlier, we found that in the xylem formation zone the sucrose level showed an upward trend from trees with slightly figured

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wood to trees with densely figured wood. The sucrose level was twice higher in the case of high figure density compared to poor figure (Novitskaya et al. 2016).

Figured wood formation and light conditions in the habitat. Karelian birch is a light-loving plant. Common habitats for naturally growing Karelian birch are abandoned farmland, forest gaps and low-density stands (Heikinheimo 1951; Yermakov 1970; Yevdokimov & Smirnov 1983). The connection between figured wood formation and light conditions in the habitat has long been known to many authors (Sokolov 1970; Lyubavskaya 1978; Yermakov 1986; Yevdokimov 1989). They emphasized in recommendations for growing Karelian birch that plantations should be made sparse, if possible, to intensify the formation of figured wood.

We explain the effect of light on figure formation in Karelian birch wood by the amount of assimilates (sucrose) supplied to the cambial zone. Limited production of assimilates is known to result in a heavier competition for photosynthetic products among consuming organs: in poor light conditions the limited amount of photosynthetic products is entirely channeled to the apical part of the shoot, causing the stem to become elongated towards the light source; when full light conditions are restored, the shading-disturbed distribution of assimilates between the top of the shoot and the roots quickly returns to the norm (Kursanov 1984). It can be concluded that the bulk of sucrose produced through photosynthesis in shaded Karelian birch trees is forwarded to the apical part of the leader shoot, shifting the growth point as close to light as possible. At the same time, there is not enough sucrose for full-scope secondary (cambial) growth and for storage metabolism and formation of storage parenchyma (= figured wood). That is why figured wood does not form in shaded Karelian birch plants. Improvement of light conditions, on the contrary, promotes the influx of large amounts of sucrose to the trunk. If the supply of sucrose to the trunk is greater than necessary for normal cambial growth, the excess would induce the development of storage tissues, i.e. figured wood. The same conclusions are valid for the case of asymmetric wood in Karelian birch plants growing at the boundary of a high density stand and a field. The tree crown is developed much better on the light-exposed side than on the side oriented towards the stand. More sucrose is supplied to the light-exposed side of the crown, promoting the formation of figured wood, whereas the sucrose level on the shaded side is only enough for a limited increment of wood with regular grain (Fig. 3 A–C).

Formation of structural abnormalities and the trunk radial growth rate. Relationship between figured wood formation and enlargement of annual wood increment in Karelian birch was first pointed out by Ruden (1954). Our data are in agreement with this observation. When explaining this phenomenon, one should remember that wide incremental layers can form only where the tissues get an ample supply of sucrose. If there is too much sucrose in the cambial zone to be fully utilized within normal cambial growth, layers of storage parenchyma begin to form, generating figured grain.

A widely known fact is that figured wood in Karelian birch can only form until a certain age (usually 40–60 years), and tissues with plain structure form on top afterwards (Lyubavskaya 1978; Yermakov 1986). Growth processes in a plant are known to slow down with age, and annual rings become visibly narrower as the tree ages. This is a result of limited supply of assimilates, which does not allow the development of storage tissues in such annual rings.

Bark thickness differences between normal and figured wood zones. Bark thickness in Karelian birch increased as wood texture grew richer.

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Living parenchyma cells, which accumulate great amounts of storage nutrients, are found nearly throughout the bark in Karelian birch (Novitskaya & Kushnir 2006). The initial substrate for these nutrients is sucrose. This fact also agrees with our belief that structural abnormalities in Karelian birch form in connection with excessive supply of assimilates to the trunk.

Pulsed development of parenchyma inclusions in Karelian birch wood. The development of an individual abnormal parenchyma layer in Karelian birch wood usually gets interrupted in spring. We believe that normal wood formation at the beginning of cambial activity is due to the fact that sugars in this period are actively utilized for crown development and therefore sucrose content in the trunk cannot be high. Hence, storage cells are not formed in the wood. As the assimilating apparatus develops, sucrose outflow from the crown intensifies and when sucrose in the trunk becomes excessive, abnormal growth resumes.

Let us note in conclusion that relying on our assumption of the regulatory role of sucrose in the formation of figured wood in Karelian birch we managed to provide a scientific explanation to quite a number of biological characteristics of this woody plant. It is for the first time that they appear as an outcome of excessive sucrose supply to the trunk rather than just as scattered facts.

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References

Ahlsved K.-J., Mandeville H. & Weissenberg K. v. [eds] (1979): Lexicon forestale. – Porvoo: Werner Söderström Osakeyhtio.

Aloni R. (2015): Ecophysiological implications of vascular differentiation and plant evolution. – Trees **29**: 1–16.

Baum S. (2001): Abbau- und Ausbreitungsstrategien holzzersetzender und endophytischer Pilze in Buche und anderen Laubbäumen. – Dr rer. nat. thesis: Germany, University of Freiburg.

Barilskaya L.A. (1978): Structural analysis of decorative wood of Karelian birch. – Bot. Zhurn. **63**: 805–811. [In Russian]

Bennett M.J., Marchant A., May S.T. & Swarup R. (1998): Going the distance with auxin: unravelling the molecular basis of auxin transport. – Philos. Trans. Roy. Soc. Lond., Ser. B **353**: 1511–1515.

Borisjuk L., Rolletschek H., Wobus U. & Weber H. (2003): Differentiation of legume cotyledons as related to metabolic gradients and assimilate transport into seeds. – J. Exp. Bot. **54**: 503–512.

Borisjuk L., Walenta S., Rolletschek H., Mueller-Klieser W., Wobus U. & Weber H. (2002): Spatial analysis of plant metabolism: sucrose imaging within *Vicia faba* cotyledons reveals specific developmental patterns. – Pl. J. **29**: 521–530.

Evert R.F. (1990): Dicotyledons. – In: Behnke H. & Sjlund R. [eds]: Sieve elements. Comparative structure, induction and development: 103–137. – Berlin & Heidelberg: Springer.

Galibina N.A., Novitskaya L.L., Krasavina M.S. & Moshchenskaya Yu.L. (2015a): Activity of sucrose synthase in trunk tissues of Karelian birch during cambial growth. – Russ. J. Pl. Physiol. **62**: 381–389.

Galibina N.A., Novitskaya L.L., Krasavina M.S. & Moshchenskaya Yu.L. (2015b): Invertase activity in trunk tissues of Karelian birch. – Russ. J. Pl. Physiol. **62**: 753–760.

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Gamalei Yu. V. (2004): Transport system of vascular plants. – St. Petersburg: Publishing House of Saint-Petersburg State University. [In Russian]

Gibson S. I. (2000): Plant sugar-response pathways. Part of a complex regularity web. – Pl. Physiol. **124**: 1532–1539.

Gibson S. I. (2004): Sugar and phytohormone response pathways: navigating a signalling network. – J. Exp. Bot. **55**: 253–164.

Heikinheimo O. (1951): Kokemuksia visakoivun kasvatuksesta. Summary: Experiences in the growing of curly birch. – Commun. Inst. Forest. Fenniae **39**(5):1–26.

Heräjärvi H. (2005): Birch - properties and utilisation. - A presentation given at COST E42 workshop, Thessaloniki, Greece. Finnish Forest Research Institute, Metla, Finland. – http://www.valbro.uni-freiburg.de/pdf/birch_prop_and_util.pdf

Hunter E. E. (1993): Practical electron microscopy. A beginner's illustrated guide. [2nd ed.] – New York: Cambridge University Press.

Ilvessalo-Pfaffli M.-S. (1995): Fiber Atlas: Identification of papermaking fibers. – Springer Series in Wood Science. – Berlin &Heidelberg: Springer.

Kedrov G. B. (2012): Functioning wood. – Wulfenia **19**: 57–95.

Koch K. E. (1996): Carbohydrate-modulated gene expression in plants. – Ann. Rev. Pl. Molec. Biol. **47**: 509–540.

Koch G. & Schmitt U. (2013): Topochemical and electron microscopic analyses on the lignification of individual cell wall layers during wood formation and secondary changes. – In: Fromm J. [ed.]: Cellular aspects of wood formation. Plant Cell Monographs 20. – Berlin & Heidelberg: Springer-Verlag.

Kosichenko N. E. & Shchetinkin S. V. (1982): Structural aspects of the hormone dependency of cambial activity disruptions. – Krasnoyarsk: Abstracts of the USSR Conference 'Problems of Woody Plants Physiology and Biochemistry'. [In Russian]

Kursanov A. L. (1984): Assimilate transport in plants. – Amsterdam: Elsevier.

Kuwajima M. (2011): Cross-linking fixatives. – Synapse Web, Kristen M. Harris (Principal Investigator) – http://synapses.clm.utexas.edu/) [Accessed 25 April 2015]

Lalonde S., Boles E., Hellmann H., Barker L., Patrick J. W., Frommer W. B. & Ward J. M. (1999): The dual function of sugar carriers: transport and sugar sensing. – Pl. Cell **11**: 707–726.

Ludwig-Müller J. (2011): Auxin conjugates: their role for plant development and in the evolution of land plants. – J. Exp. Bot. **9**: 1–17.

Luostarinen K. & Verkasalo E. (2000): Birch as sawn timber and in mechanical further processing in Finland. – Silva Fenn. Monogr. **1**.

Lyubavskaya A. Ya. (1978): Karelian birch. – Moscow: Publishing House Forest Industry.

Michalczuk L. & Bandurski R. S. (1982): Enzymic synthesis of 1-O-indol-3-ylacetyl-b-D-glucose and indol-3-ylacetyl- myo-inositol. – Biochem. J. **207**: 273–281.

Mishra B. S., Singh M., Aggrawal P. & Laxmi A. (2009): Glucose and auxin signaling interaction in controlling *Arabidopsis thaliana* seedlings root growth and development. – PLoS ONE **4**(2): e4502.

Novitskaya L. L. (1997): About a possible cause of formation of Karelian birch structural abnormalities. – Bot. Zhurn. **82**: 61–66. [In Russian]

Novitskaya L. L. (2008): Karelskaya bereza: mekhanizmy rosta i razvitiya strukturnykh anomaliy (Karelian birch: mechanisms of growth and development of structural abnormalities). – Petrozavodsk: Publishing House Verso. [In Russian]

Novitskaya L. L., Galibina N. A. & Nikerova K. M. (2015): Sugar transport and storage in the phloem of *Betula pendula* Roth var. *pendula* and var. *carelica*. – Trudy Karelsk. Nauch. Tsentr. RAN **11**: 35–47.

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Novitskaya L. L. & Kushnir F. V. (2006): The role of sucrose in regulation of trunk tissue development in *Betula pendula* Roth. – J. Pl. Growth Regulat. **25**: 18–29.

Novitskaya L. L., Nikolaeva N. N., Galibina N. A., Tarelkina T. V. & Semenova L. I. (2016): The greatest density of parenchyma inclusions in Karelian birch wood occurs at confluences of phloem flows. – Silva Fenn. **50**(3): article id 1461. – http://dx.doi.org/10.14214/sf.1461

Price A. & Macdonald E. (2012): Growing birch in Scotland for higher quality timber. – Internal report to FC Scotland. – http://www.forestry.gov.uk/fr/infd-6wdc49

Rolland F., Moore B. & Sheen J. (2002): Sugar sensing and signalling in plants. – Pl. Cell **14**: 185–205.

Ruden T. (1954): Om valbjork og endel andre unormale veddannelser hos bjork. – Meddel. Norske Skogsforsøksvesen **12**(43): 451–505.

Schwarze F. W. M. R. (2007): Wood decay under the microscope. – Fungal Biol. Rev. **21**: 133–170.

Schwarze F. W. M. R., Baum S. & Fink S. (2000): Dual modes of degradation by *Fistulina hepatica* in xylem cell walls of *Quercus robur*. – Mycol. Res. **104**: 846–852.

Shchetinkin S. V. (1987): Histogenesis of figured wood in birch (*Betula pendula* Roth. var. *carelica* Merkl. and *Betula pendula* Roth.). – Cand. of Biology (PhD) Thesis: Univ. Voronezh. [In Russian]

Sheen J., Zhou L. & Jang J. C. (1999): Sugars as signalling molecules. – Curr. Opin. Pl. Biol. **2**: 410–418.

Shnawa H. A., Muhsen M. G., Aldaeem D. A., Ibraheem I. K., Gumaa F. M. & Saleh A. I. (2011): Synthesis of barium tannate from eucalyptus bark and its use as a thermal stabilizer for polyvinyl chloride. – BioResources **6**: 700–706.

Simko I. (1994): Sucrose application causes hormonal changes associated with potato tuber induction. – J. Plant Growth Regul. **13**: 73–77.

Singh M., Gupta A. & Laxmi A. (2014): Glucose control of root growth direction in *Arabidopsis thaliana*. – J. Exp. Bot. **65**: 2981–2993.

Smeekens S. (2000): Sugar-induced signal transduction in plants. – Ann. Rev. Pl. Physiol. Pl. Molec. Biol. **51**: 49–81.

Sokolov N. O. (1970): Selection and cultivation of Karelian birch in the Leningrad Region using natural seeding. – In: Yermakov V. I. [ed.]: Forest genetics, selection and seed production: 277–281. – Petrozavodsk: Publishing House Karelia.

Srebotnik E. & Messner K. (1994): A simple method that uses differential staining and light microscopy to assess the selectivity of wood delignification by white rot fungi. – Appl. Environment. Microbiol. **60**: 1383–1386.

Thiéry G., Bernier J. & Bergeron M. (1995): A simple technique for staining of cell membranes with imidazole and osmium tetroxide. – J. Histochem. Cytochem. **43**: 1079–1084.

Wobus U. & Weber H. (1999): Sugars as signal molecules in plant seed development. – Biol. Chem. **380**: 937–944.

Yermakov V. I. (1970): Karelian birch propagation by grafting. – In: Yermakov V. I. [ed.]: Forest genetics, selection and seed production. Petrozavodsk: Publishing House Karelia. [In Russian]

Yermakov V. I. (1986): Mechanisms of adaptation of birch in the North. – Leningrad: Publishing House Nauka. [In Russian]

Yevdokimov A. P. (1989): Karelian birch biology and cultivation. – Leningrad: Leningrad University publishers. [In Russian]

Yevdokimov A. P. & Smirnov S. D. (1983): Growing Karelian Birch in the North-west of RSFSR. – Leningrad: Leningrad University publishers. [In Russian]

Xu X., van Lammeren A. A. M., Vermeer E. & Vreugdenhil D. (1998): The role of gibberellin abscisic acid and sucrose in the regulation of potato tuber formation *in vitro*. – Pl. Physiol. **117**: 575–584.

Yu S.-M. (1999): Cellular and genetic responses of plants to sugar starvation. – Pl. Physiol. **121**: 687–693.

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