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CURRENT TRENDS IN THE STRUCTURAL INVESTIGATIONS OF THE VASCULAR CAMBIUM

Współczesne trendy w badaniach strukturalnych kambium

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ABSTRACT

The study of the structure of the vascular cambium is of fundamental importance to deepening knowledge of the secondary growth of woody plants. Since it helps to understand the influence of internal and external environmental factors of tree growth on the quality of wood, it has also a practical value. Structural investigations of the vascular cambium can be divided into three main groups a) descriptive, b) developmental and c) applied. This short review points out problems connected with the research of the structure of cambium bring up in contemporary literature.

INTRODUCTION

The vascular cambium¹ is a meristematic tissue responsible for secondary growth of trees, which comprise over 90% of the terrestrial biomass on the earth (Berlyn and Ashton 1996). Meeting the increase demands for forestry products is likely to require increased forest productivity. The full understanding of the cambial structure allows to obtain plantation of trees characterised by wood of high utility value.

The study of the structure of cambium can be classified into macroscopic and microscopic investigations. Macroscopic investigations use

tree morphology for the interpretation of cambial structure, whereas microscopic studies are focused mainly on details of cambial structure. Microscopic structural investigations of cambium can be subdivided into three groups: a) descriptive, b) developmental and c) applied. The aim of this article is to indicate the current problems in these groups of microscopic investigations of cambium.

DESCRIPTIVE STUDIES OF CAMBIAL STRUCTURE

These research focus on the fundamental principles of microscopic structure, e. i. the patterning of tissue and cell types, as well as the cell-specific properties of specialised cell types (Rajput and Rao 1998; Rajput 2003). Here belong also investigations describing changes in cambial structure during seasonal cambial activity (Rao and Rajput 2001). All these information are a source of data for classification (comparative studies), and are the initial base of developmental, applied as well as genetic studies of cambium. The novelty in such classical field of research is applying of new research tool, like confocal laser scanning microscope (Funada et al. 2000; Kitin et al. 2000, 2002). It means that laborious and time-consuming preparations sections of resin-embedded tissue can be replaced by use of the confocal micro-

¹ The vascular cambium is a lateral meristem that produces the secondary phloem and xylem. It is a heterogeneous tissue compounds of two types of cells, the elongated fusiform cells and the nearly isodiametric ray cells, which form rays. The arrangement of fusiform initials can be non-storeyed, storeyed or double-storeyed (when storeyed arrangement of fusiform cells is accompanied by storeyed arrangement of rays).

scope, which provided a quick and easy method for visualisation of the 3-D structure of cambium in thick hand-cut sections.

DEVELOPMENTAL STUDIES OF CAMBIAL STRUCTURE

It is possible to considerate developmental changes in the structure of the vascular cambium with reference to a few processes. The first one is connected with the transition from procambium to cambium. The second one is associated with the mechanisms of the formation of non-storeyed, storeyed or double-storeyed cambium. The third one concerns the way of the rearrangement of initials in all types of cambium. Developmental studies are being carried out with use of: direct method (e. i. research on the active cambium), indirect method (e. i. research on the xylem which mirrors structure of the cambium) and models.

The way of consideration of cambium, as two-dimensional or three-dimensional tissue, imposes the way of the interpretation of developmental processes in this tissue. It is worth noting that in studies of cambium with application of direct and indirect method the way of consideration of cambium has changed from two-dimensional into three-dimensional. This change gave an opportunity for a new interpretation of cambial events like intrusive growth and in a consequence provides fresh clues on the cambial dynamics. Study of the cambium of *Pinus sylvestris* (Włoch et al. 2002), *Tilia cordata* (Włoch and Połap 1994) and *Wisteria floribunda* (Kojs et al. 2004b) demonstrated that intrusion of the elongating initial in fact takes place along periclinal walls of adjacent fusiform initial and its immediate derivative. Intrusive growth of the fusiform initial was found to begin with development of characteristic *slants* (observed in transverse sections of an active cambium), representing a transitional stage of the process of transformation of periclinal walls of fusiform initial cells into radial walls (Jura and Włoch 2003; Włoch et al. 2005; Kojs et al. 2005). The gradually progressing event comprised (a) appearance of either a tri-

angular microspace limited by two periclinal walls of a fusiform initial and its derivative and one radial wall of another fusiform initial in the adjacent radial file, or a rhomboidal microspace enclosed by four periclinal walls of two laterally adjacent fusiform initials and their immediate derivatives, (b) intrusion of elongating tip of fusiform initial from neighbouring file into the microspace thus formed, (c) symplastic growth of the cambial cell walls in radial direction, (d) unequal periclinal divisions of fusiform initial cells while growing intrusively, and (e) unequal periclinal divisions of derivative cells not growing intrusively. This interpretation rejects the hitherto held concept that intrusive growth of fusiform initial occurs between the radial walls of adjacent initials.

Study of the cambium with application of indirect method provided information that the mechanism of the rearrangement of cambial initials leading to the formation of spiral grain² in the wood of *Pinus sylvestris* characterises non-storeyed cambium (Włoch et al. 2002), as well as interlocked grain in wood of tropical trees like *Lonchocarpus sericeus*, which possesses double-storeyed cambium (Kojs et al. 2003, 2004a) is connected with the intrusive growth of one initial cell between periclinal walls of the neighbouring initial and its immediate derivative.

Pattern formation in the vascular cambium is considerate also with applying of models. Mathematical model was used to describe the dynamic of fusiform initial cells orientation, and their interaction with the auxin (Kramer 2002). It was also worked out a mathematical model by means of it is possible to predict the frequencies of anticlinal and periclinal cell divisions (Barlow et al. 2002). An attempt of simulating the production of xylem also has been made (Forest et al. 2004) as well as mathematical analysis of whirled grain in cottonwood trees (Kramer 1999; Kramer and Groves 2003).

The authors describing mathematical models of pattern formation in the vascular cambium of trees consider cambium in two dimensions. Barlow et al. (2002) and Forest et al. (2004) take into consideration tangential and radial

² The degree of inclination and the rate of the change in orientation of the cambial initials determine the same changes of its derivatives (phloem and xylem). Changes in location of axial wood elements create 'wood grain', which can be straight, spiral, wavy or interlocked.

dimension, whereas Kramer (2002) and Kramer and Groves (2003) tangential and axial dimension. These authors usually define cambium as a layer only one cell thick, that forms a continuous cylindrical sheath around the trunk and the branch, so they simplify consideration of this tissue from three dimensions to two.

The relationship between model and real system is similarity. To understand the mechanism of rearrangement of initial cells, surrounded by adjacent cells in all directions seems necessary describing cambium in three-dimensional space. In phenomenological models of cambium this assumption was taken into consideration. The models concern the probable patterns transformation of non-storeyed arrangement of fusiform initials into the storeyed one and the mechanism of cambial cells rearrangement (Kojas et al. 2002, 2004b, 2005; Jura and Włoch 2003). It was assumed that cambial cells rearrangement is strictly connected with changes in the patterns of mechanical stresses and proposes existence of a system, based on the negative feedback, for the control of cambial cells rearrangement. This system includes relations between all cell events and the tension, compression and shear stresses, showing the plurality of environmental modifiers of the process. The proposed hypothesis considers the cambium as an early-warning, self-regulating system, which enables the tree to adapt its structure to the constantly changing conditions of the internal and external environments.

APPLIED STUDIES OF CAMBIAL STRUCTURE

The fundamental knowledge obtained on the base of descriptive and developmental studies of cambium allows checking the influence of different kind of factors on its structure. It can be environmental factors (Kurczyńska et al. 1997, 1998; Tulik 2001) or pathological factors e. i. bacteria or fungi (Aloni et al. 1995; Włoch et al. 2001; Sakamoto et al. 2004).

Combination of descriptive, comparative and developmental studies of cambial structure can help identify its function. Cambium is responsible for secondary thickening of trees and for the quality of wood. From non-storeyed cambium it is possible to arise straight, spiral or wavy grained wood, while interlocked grain is

formed only by double-storeyed cambium. The double-storeyed arrangement of cambium enable forming interlocked grain in wood, which next enable fast growth of a tree in conditions of strong competition for light, with maintenance of the mechanical properties of the a trunk (Kojas et al. 2002). That is why over 80% of trees growing in the canopy and emergent layers of tropical rainforests possess double-storeyed cambium (Kojas et al. 2003; Iqbal et al. 2005).

In spite of progress of research techniques and in recent years very rapid development of genetics studies of woody plants, structural investigations seems to have large meaning in development of knowledge on cambium. Structural investigations of cambium make the basis for majority of model research and because of that are also base and point of reference of physiological and molecular investigations.

STRESZCZENIE

Badania struktury kambium mają fundamentalne znaczenie poznawcze związane z pogłębieniem wiedzy na temat przyrostu wtórnego roślin drzewiastych oraz znaczenie praktyczne, bowiem pomagają lepiej zrozumieć, w jaki sposób czynniki środowiska wewnętrznego i zewnętrznego rosnącego drzewa wpływają na jakość pozyskiwanego drewna. Wśród badań strukturalnych kambium wyróżniono: a) badania opisowe, b) badania rozwojowe oraz c) badania stosowane. Celem artykułu jest wskazanie problemów związanych z badaniami struktury kambium, którym poświęca się dużo uwagi we współczesnej literaturze.

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