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Citation style: Hejnowicz Zygmunt, Kurczyńska Ewa U. (1987). Occurrence of circular vessels above axillary buds in stems of woody plants. "Acta Societatis Botanicorum Poloniae" (1987, nr 3, s. 415-419).

ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 56, nr 3: 415–419
1987

Occurrence of circular vessels above axillary buds in stems of woody plants

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(Received: April 3, 1987. Accepted: April 8, 1987)

Abstract

The circular vessels generally occur in intact wood stems just above the axillary buds. In this region the cell arrangement with vortices occurs. We interprete the circular vessels as the result of circular polarity in the cambial zone of the region above the axillary bud. The stability of circular polarity in this region is based on the vorticity of the cambium cells arrangement.

Key words: circular vessel, circular polarity

INTRODUCTION

An extremely interesting feature of vascular differentiation in plants is a formation of circular vessels in the form of closed rings (Sachs and Cohen 1982), because this phenomenon has a profound meaning for understanding of polarity, polar differentiation and involvement of auxin or other regulators in these processes in plants (Sachs 1984, Mitchison 1981). The circular vessels are common in wounded organs and isolated tissues, especially in experiments involving isolation and treatment with auxin, but they were observed also in untreated storage organs (Sachs and Cohen 1982) and in abnormal stems in *Ficus* (Aloni and Wolf 1984). The occurrence of circular vessels was found by Sachs and Cohen to be predictable: 1) the vessels occur above the level where polar continuity is interrupted or sharply restricted; 2) the formation of circular vessels resembles that of normal vessels in being promoted by developing shoot or exogenous auxin source on apical side, however circular vessels were never observed close to the place of auxin application; 3) initiation of adventitious roots above the cut reduces circular vessel formation there and treatments that inhibit root initiation increase the number of circular vessels; 4) when stems of bean plants were incised obliquely from opposite sides, so that the transport in the tissue maintaining the continuity between the apical and basal part was inverted, circular vessels were formed in the tissue. Similarly, circular vessels occurred in grafts when one of the graft members was inverted. We study the formation of vessels in stem segments of *Fraxinus excelsior* (which will be reported in another paper) and during these studies we noticed that there are circular vessels in normally growing stems above the axillary buds. Thereafter we looked whether similar phenomenon occurs in other plants and we found it as a quite common one. The purpose of this paper is the presentation of this phenomenon.

MATERIAL AND METHODS

The material was collected in June, 1986. One year old stems of *Fraxinus excelsior*, *Quercus robur*, *Acer pseudoplatanus*, *Acer platanoides*, *Tilia cordata*, *Betula verrucosa*, *Populus nigra* and *Sorbus aucuparia* were used. The stems were cut into segments each comprising a node. The bark tissues were removed and the remaining sticks of wood were first immersed in ethanol solution of phloroglucin for 2–3 minutes, then in concentrated HCl for several seconds and finally they were washed in tap water. The sticks were examined under a stereomicroscope. We payed special attention to the area which was just above the auxillary bud. We made the tangential sections by hand for microscopic investigations. The sections were put on microscopic slides in lactic acid. In the case of *Fraxinus excelsior*, one year old stems were collected in winter, too. We made a series of tangential sections comprising secondary phloem, cambium and secondary wood just above the axillary bud.

RESULTS

FRAXINUS EXCELSIOR

Figure 1 shows the position of occurrence of the circular vessels; it is just above the axillary bud. The size of the area within which

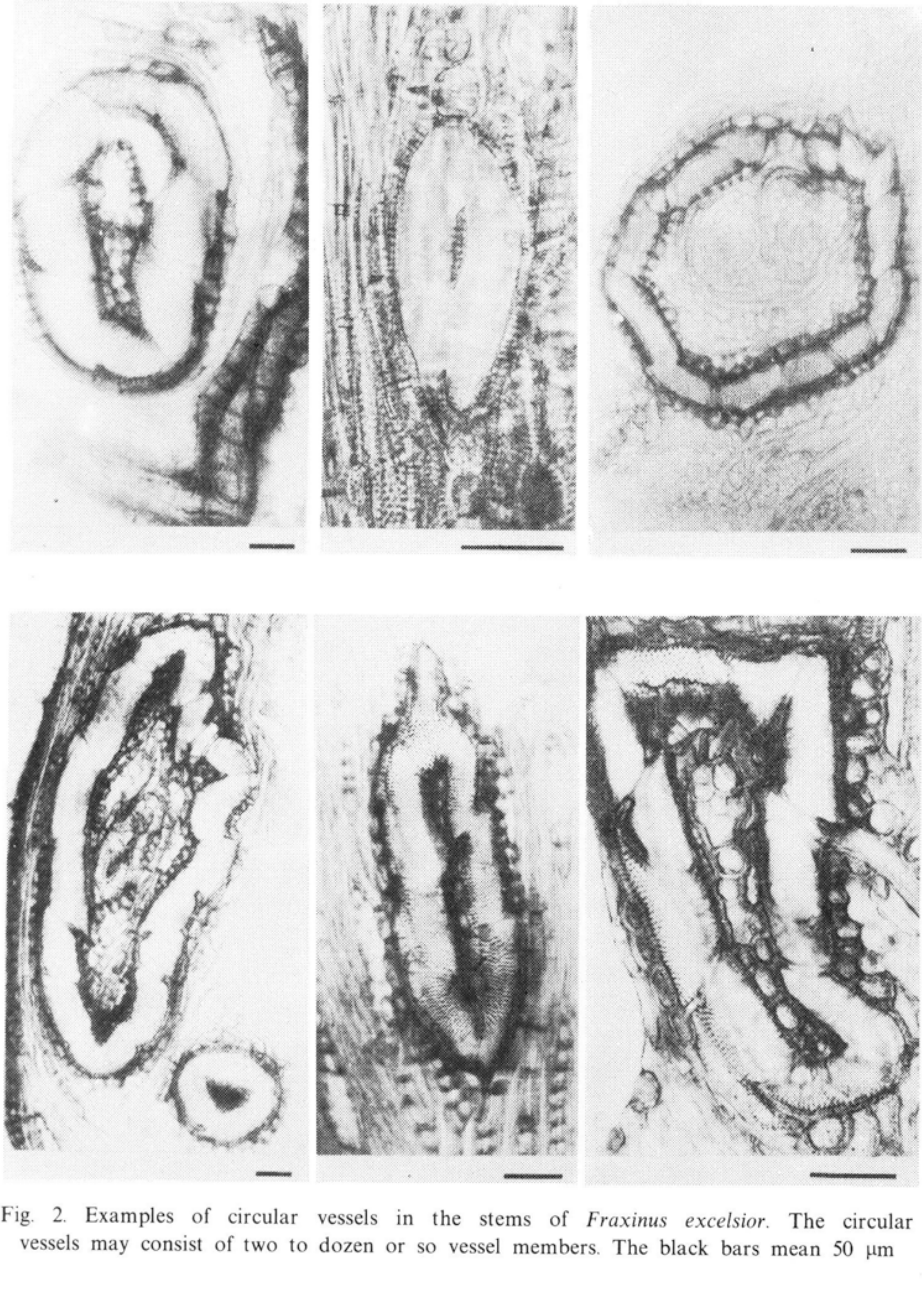

Fig. 2. Examples of circular vessels in the stems of *Fraxinus excelsior*. The circular vessels may consist of two to dozen or so vessel members. The black bars mean 50 μm

Fig. 3. The tangential section of the region above the auxillary bud. X-figures (x), vortices (v) and circular vessels (cv) are visible. The black bar mean 100 μm

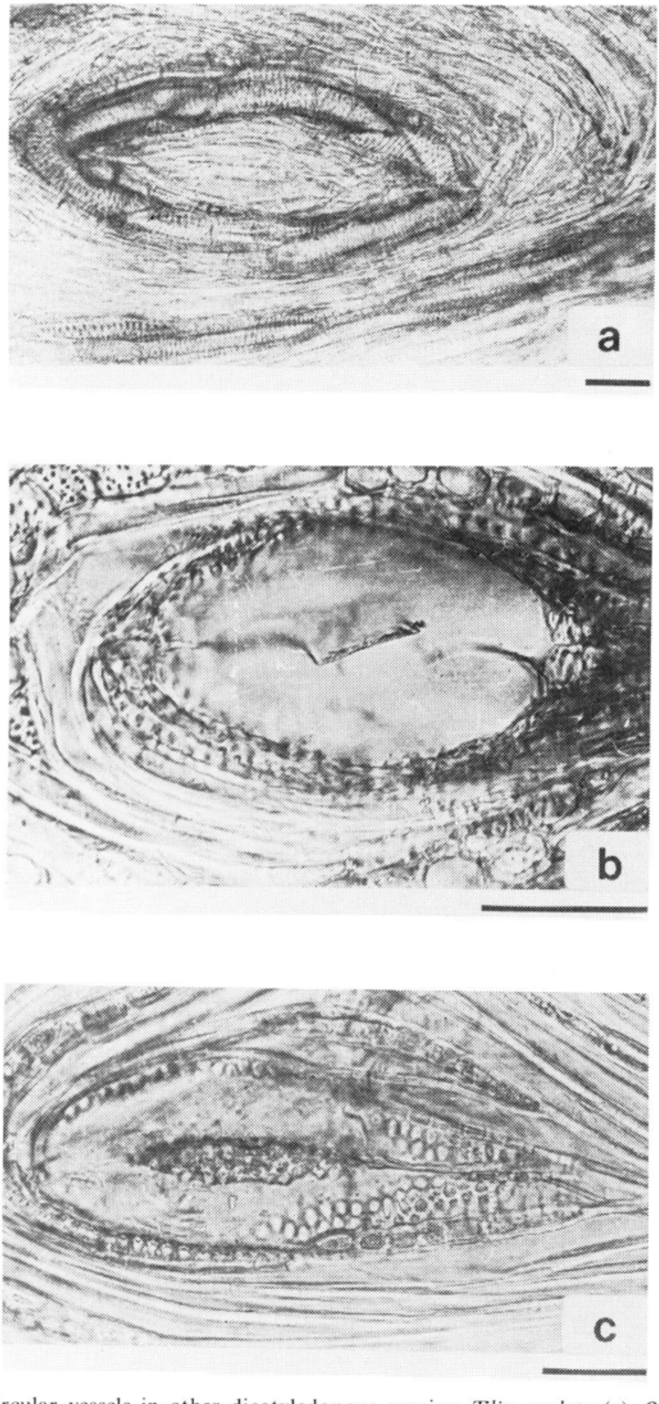

Fig. 4. The circular vessels in other dicotyledonous species: *Tilia cordata* (a), *Quercus robur* (b) and *Populus nigra* (c). The black bars mean 50 μm

circular vessels may occur is about 2 mm^2 and does not seem to change apparently during the first year of stem life. Figure 2 shows examples of circular vessels. A vessel involves 2 to more than a dozen vessel members. There may be more than one circular vessel above the axillary bud. The vessel members of a circular vessel qualitatively are the same as those of normal vessels. Their length is usually shorter which is due to shorter cambial initials. The diameter is variable, but may attain value a few times higher than that of the tangential diameter of cambial initial. The region of circular vessel occurrence is already characterized in the cambium by a complicated pattern of cell arrangement which

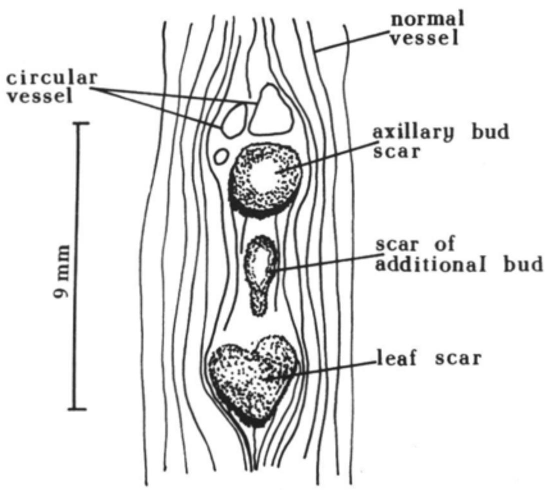

Fig. 1. The location of circular vessels

has qualitative appearance of streamlines of flow passing a stationary body; there are vortices and x-figures of cells (stagnation points in hydrodynamic terminology) within this region (Fig. 3). The arrangement of cambial cells is maintained both by the secondary xylem and phloem produced by these cells with only little modifications resulting from growth in width and intrusive growth of differentiating cells.

The circular vessels occur within the vortices: the size of a circular vessel within the same vortex may be different in a different layer. A circular vessel is never connected by vessel members with a non-circular vessel. In the case of two-member circular vessels there is always a ray inside. Most rays within the region of occurrence of the vortices and x-figures are of abnormal shape. Fibers within this region have normal appearance as regards the cell wall thickness, however their shape is determined by the shape of the cambial initials. There seems to be much less intrusive growth during their differentiation than in the case of normal fibers within the wood containing normal vessels.

OTHER DICOTYLEDONOUS SPECIES

Qualitatively the arrangement of cambial cells and occurrence characteristics of circular vessels in *Quercus robur*, *Acer pseudoplatanus*, *Acer platanoides*, *Tilia cordata*, *Betula verrucosa*, *Populus nigra* and *Sorbus aucuparia* is similar to those in *Fraxinus excelsior* (Fig. 4).

DISCUSSION

There are good reasons to interprete the formation of vessels, whether normal or circular, as resulting from the flux of auxin and perhaps from other yet unknown inductive signals (Sachs 1984). Sachs developed the hypothesis that the vascular differentiation follows the polar flow of the signals, of which one is auxin, and that there is positive feedback between polarity, flow and differentiation. Polarity determines the direction of flow of auxin and the flow is necessary to maintain the polarity. If the direction of the flow of auxin is changed locally the polarity may be changed in a positive feedback manner. The new polarity diverges from that previously established in the direction of the route of expected diffusion or in other form of auxin transport and the further auxin flow follows this new polarity. In the differentiating xylem auxin flow seems to be canalized to the defined files of cells and this canalized flow is considered to be a main factor inducing vessel differentiation. The axis of a vessel indicates thus polarity axis (direction without arrowhead) which is termed axiality (Sachs 1984). Normal vessels (having two ends) develop when canalized polar flow of auxin leads from a sink to the source. The circular vessels are interpreted as resulting from the flux which follows a circular route. The polarity underlying this flow would be represented in the line of arrows bent into a closed loop so that the polarity is either clock- or anticlockwise. We assume that the Sachs's hypothesis is valid also in the case of circular vessels above axillary buds and that the vessels represent circular polarity there. An intriguing feature of this polarity is its stability: the circular vessels appear again and again in the nearly the same position which means that the circular polarity is maintained. Stable circular polarity is a novel phenomenon. Probably the stable circular polarity characterizes already the cambium in the considered region; this is the simplest explanation of the vortical arrangement of cambial cells. Such arrangement of cambial cells may form the structural basis for the circular polarity within the cambium. If the circular polarity is bound in positive feedback with auxin transport a question appears how the auxin flows through the considered region.

Maybe there is a vortex in this flow within the cambium plane and further forward flow follows the direction normal to this plane for instance through the rays. Interesting problems are the development of the vortical arrangement of cambial cells and the functional role of the vortical structures above the axillary buds.

Acknowledgment

This work was supported in part by grant 04–01 from the Polish Academy of Sciences.

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Występowanie kołowych naczyń nad pąkami pachwinowymi w łodygach roślin drzewiastych

Streszczenie

Kołowe naczynia występują powszechnie w nienaruszonych łodygach drzew tuż nad pąkami pachwinowymi. W regionie tym w kambium występuje zawirowany układ komórek. Naczynia kołowe interpretujemy jako wyraz kołowej polarności w kambium nad pąkiem pachwinowym. Stabilność polarności kołowej w tym regionie zasadza się na zawirowaniu układu komórek kambium.