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ON INTERCELLULAR SPACES IN THE XYLEM RAY PARENCHYMA OF PICEA ABIES

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SUMMARY

The radially-running intercellular spaces in ray parenchyma of adult xylem of *Picea abies* were studied with the light microscope and with the scanning electron microscope. Special attention was paid to radial continuity and dimensions of these channels, and also to the blind pits in the parenchymatous cell walls opposite these intercellular spaces. In locally very thick-walled ray parenchyma, an aberrant type of blind pitting seems to occur.

1. INTRODUCTION

The structure and function of radial intercellular spaces in ray parenchyma has been the subject of several publications. BACK (1969), GODWIN & GODDARD (1940), MOLLER & MÜLLER (1938), REDIES (1962) and RUSSOW (1883) stressed their function in respiration. Russow even went so far as to consider these intercellular spaces as part of a whole system running uninteruptedly through cambium, bark, and other tissues to connect the woody tissues through lenticels with the outer atmosphere. The occurrence of radial intercellular spaces has been reported for many woods (BACK 1969, ESAU 1960, GREGUSS 1955, NYREN & BACK 1960, PANSHIN & DE ZEEUW 1970, RUSSOW 1883) and may be considered to be a general phenomenon. According to REINDERS & REINDERS-GOUWENTAK (1961) the spaces originate by splitting of the middle lamella and are therefore schizogenous. Pectinous rims may be present at the corners or as small projections on the sides of the, mostly, triangular spaces as seen in longitudinal tangential sections. PANSHIN & DE ZEEUW (1970) report cross sectional dimensions ranging from 1 to 15 sq. microns in the tangential plane.

The radial intercellular spaces are connected with the ray parenchyma cells through blind pits at the corners of the ray cells (BACK 1969, RUSSOW 1883, I.A.W.A. 1964).

More detailed knowledge of structure and distribution of the intercellular spaces and the blind pits in *Picea abies* is important for timber technology (e.g. penetration of preservatives, strength properties) and has also some general wood anatomical relevance.

The rays in *Picea abies* are exclusively uniseriate, except the scarce fusiform ones which contain resin canals.

2. MATERIAL AND METHODS

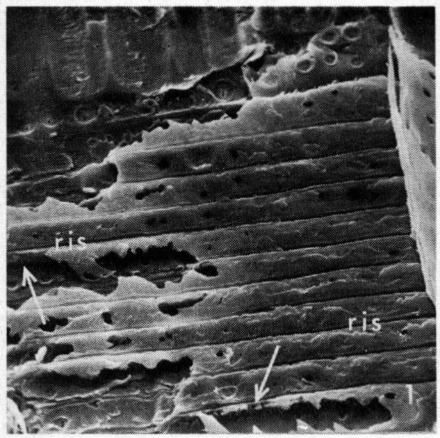
Radial and tangential longitudinal sections, as well as oblique radial and tangential sections from the heartwood of *Picea abies* Karst. (Norway spruce), were cut for light microscopy. Sections were stained with 0.5% Astrablue in 2% tartaric acid and with 0.5% aquous Astrazon Red. Sections from small blocks, which were pre-vacuum-impregnated with 0.1N silver nitrate and after drying with hydrochloric acid vapour, were also studied. For scanning electron microscopy (S.E.M.) the radial longitudinal plane was obtained by splitting. Surfaces in the tangential longitudinal as well as in oblique radial and oblique tangential planes were obtained with a sledge microtome from Carbowax (1500) embedded small air-dried samples of Spruce heartwood. All specimens were tested on the presence of compression wood; only material free from this defect was used for investigation.

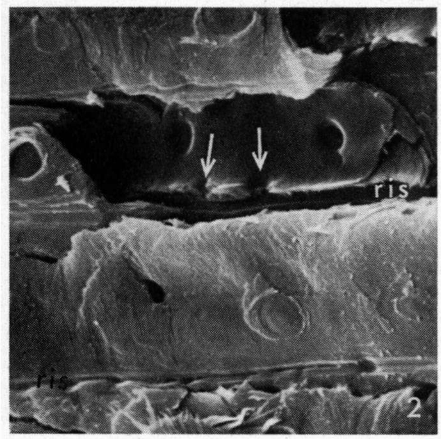
3. RESULTS

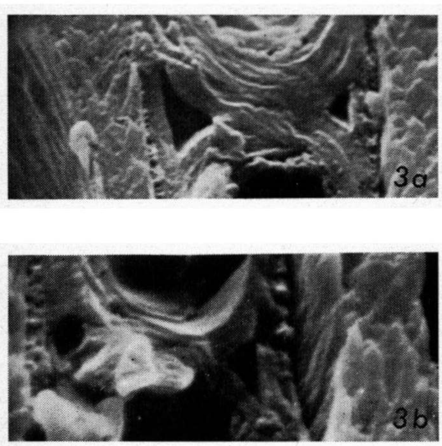
3.1. The intercellular spaces

Radial longitudinal as well as tangential longitudinal planes give most structural detail of the radial intercellular spaces. In S.E.M. pictures small radially long-running canals parallel to the edges of the parenchyma are clearly visible in radially split surfaces, where the cells have split along the middle lamella (*fig. 1*). Such spaces have been found between all ray parenchyma cells observed. There are no distinct structures of any kind which may point to clogging of these long-running spaces. They seem to be quite uniform. However, with the light microscope one can demonstrate widenings of the intercellular spaces near the end walls of the parenchyma cells (through rounding of the corners of these cells), in scanning electron micrographs these widenings are less clear (see, however, *fig. 7*). In the tangential plane the shape of radial intercellular spaces is more or less triangular, lined as they are by longitudinal tracheids and two oblique portions of the horizontal-radial ray cell wall (*fig. 3*). Cross-sectional measurements of radial intercellular spaces result in 2 to 3 (rarely 1 to 8) sq. microns. Observations at the growth ring boundaries point to a continuous nature of the intercellular spaces, without any transformation. Staining with Astrablue mostly gives a dark blue lining on the inner side of the intercellular spaces, probably corresponding with a pectic layer.

The presence or absence of radial intercellular spaces between ray parenchyma and ray tracheids was also examined. S.E.M. pictures did not provide any information about this and with the light microscope no absolute proof of absence or presence could be given. In an estimated 5 per cent of the rays very small, more or less circular intercellular spaces between the corners of parenchymatous and tracheidal elements of the rays occur (T.L. section). However, these spaces appear wholly or partly clogged with pectinous substance. R.L. sections do not indicate a long-running radial course of intercellular spaces between ray tracheids and parenchyma cells.







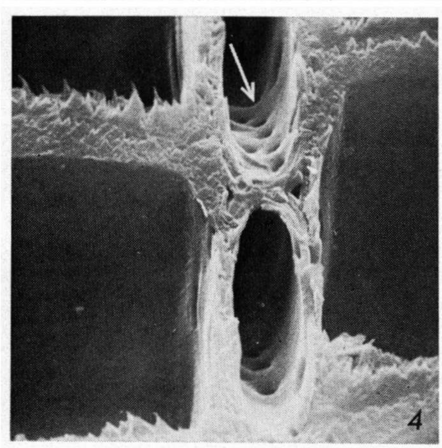


Fig. 1. Radially split surface of xylem ray parenchyma. Blind pits (arrow) occurring opposite to the radially long-running intercellular spaces (r.i.s.). S.E.M. × 275.
Fig. 2. Radially split surface of ray parenchyma cells. Blind pits (arrow) debouching into radial intercellular space (r.i.s.). S.E.M. × 1,100.
Fig. 3. Oblique tangentially microtomed surface of two ray parenchyma cells showing: (a) triangular shape of radial intercellular spaces, varying in cross-sectional width; (b) on the left the less regularly occurring oval form of radial intercellular space. Observations with the light microscope support the view that the outline illustrated here is not artefactual. S.E.M. × 2,750.
Fig. 4. Oblique tangentially microtomed surface of ray parenchyma. Note in upper cell the straight-lined orientation of the blind pits. S.E.M. × 1,100.

3.2. The blind pits

In studying radial longitudinal surfaces of ray parenchyma with the scanning electron microscope two types of blind pitting can be distinguished:
a) irregularly oriented pits not occurring opposite the intercellular spaces; this type of pit only sporadically occurs in cell wall parts which are exceedingly and irregularly thickened, mostly situated in or near the horizontal-radial wall.

b) rather regularly oriented pits opposite the intercellular spaces.

For timber technological aspects pits of the last category (b) seem to be the most important ones and are therefore given special attention in this study (*figs. 2, 4*).

In areas of radially split surfaces where the horizontal-radial parenchyma cell walls have been broken off and the radial intercellular spaces have been exposed the contours of blind pits can be observed (*fig. 2*). The outer aperture is somewhat wider than the inner one. In general the diameter of the pit membrane is about half of the depth of the pit, but may vary depending on cell wall thickness (*fig. 5*). Scanning electron micrographs of oblique tangential and oblique radial planes give good information on the orientation of the blind pits. For the greater part the blind pits are arranged in a straight line in the rounded part between the vertical-radial and horizontal-radial cell wall (*figs. 4, 5, 6*). In the light microscope the blind pits in adjacent parenchyma cells were usually found to correspond with each other, but for the intervening intercellular space.

It is interesting to compare number and size of blind pits with those of the other simple pits in ray parenchyma of *Picea abies* (*table 1*).

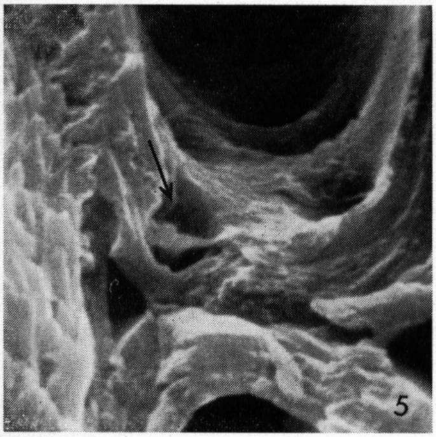
Table 1.

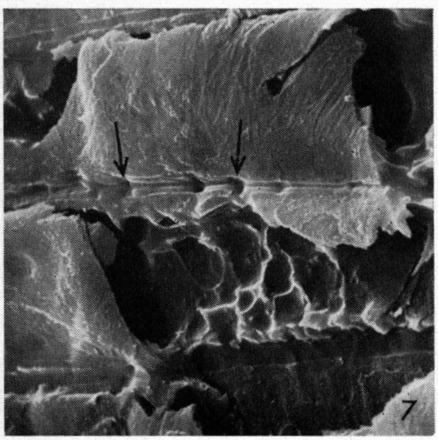
direction of parenchyma cell wall	type of pits*	average pit diameter (μm)	frequency of pits per 100 μm cell wall length
vertical-radial[a]	simple[1]	2	10
horizontal-radial[a]	,, [2]	1.5–2	20–25
to intercellul. space[a]	,, [3]	1.5–2	20–25
,, ,, ,, [b]	,, [3]	1.5	30–45

* forming part of: [1]half-bordered pit-pair, [2]simple pit-pair, [3]blind pit; [a]NYREN & BACK (1960); [b]LAMING (1972).

It may occur that curious, trumpet-like structures are found in the radial plane (*fig. 7*). These structures look like hollows debouching from the parenchyma side into the radial intercellular spaces. Locally the outer aperture of the trumpet-like structures may be of the same diameter as or even wider than the vertical plane delimiting the intercellular space. These structures are only found between locally very thick-walled parenchyma cells, and the sides of the intercellular spaces are then always creased on the parenchyma side. The creases are continuous in the trumpet-like hollows. Because of the unusual orientation and frequency of this type of structure it is suggested that it may be considered as a particular type of blind pitting. However, structural units like pit membrane and pit aperture could not be observed during this study.

Based on joint experiences obtained from preceding studies and from literature data a schematic representation applicable for *Picea* and illustrating a partial





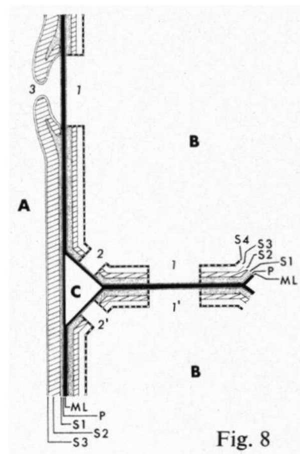


Fig. 5. Oblique tangentially microtomed surface showing sectioned pit chamber of a blind pit (arrow). S.E.M. × 5,500.

Fig. 6. Oblique radially microtomed surface showing a radial intercellular space (arrow) with belonging blind pits (1). In the inner of open-laid parenchyma cell are noteworthy: (1) blind pits and (2) simple pits forming part of pit-pairs. S.E.M. × 1,100.

Fig. 7. Radially split surface of thick-walled ray parenchyma. Trumpet-like structures (arrow) debouching from parenchyma side into "creased" radial intercellular space are visible. S.E.M. × 1,100.

Fig. 8. Schematic representation (longitudinal tangential) of cell walls of a longitudinal tracheid (A) and of ray parenchyma cells (B) enclosing a radial intercellular space (C). Because of clearness the middle lamella (ML) has been thick-lined. Different types of pitting are marked: 1 and 1′, simple pits forming a simple pit-pair; 2 and 2′, blind pits abutting on radial intercellular space; 3, bordered pit, forming a half-bordered pit-pair by pairing a simple pit (1).

tangential section of ray parenchyma and a longitudinal tracheid has been designed (*fig. 8*). Types of pitting and cell wall layers are indicated. For the parenchyma cell wall structure the model of Harada & Wardrop (1960) was maintained and adjusted for *Picea* as far as the membrane of the half-bordered pit-pair is concerned. Models of WARDROP (1964) and of JUTTE & SPIT (1963) underlie the schemes for the tracheid cell wall and for the bordered pit, respectively.

4. DISCUSSION

The results of this study are in general agreement with earlier reports in the literature (see introduction). In the first place they are additional to these earlier publications as far as the three-dimensional structure of the radial intercellular spaces and structure and distribution of blind pits are concerned. The current opinion that blind pits are essentially similar to the pits in ordinary simple pit-pairs is fully supported by this study.

It may be interesting to compare *Picea* with another member of the *Pinaceae*: *Pinus*, which has much different ray parenchyma. BACK (1969) found for *Pinus sylvestris* a significantly higher percentage of the mean relative volume of the gas canal system for wood as a whole and for ray parenchyma alone than in *Picea abies*. However, the percentage of parenchyma cells of the ray volume is equal in both genera. In contrast to the circular blind pits in *Picea*, Back observed slit-like pits to the radial intercellular spaces in *Pinus*. The mean cross-sectional area of the intercellular spaces in *Pinus* is ten- to fifteenfold that in *Picea*.

The relevance of these structural differences for impregnation, e.g. with preservatives, will be the subject of a future paper.

The structure of intercellular spaces and blind pits invites speculations about their mode of origin and possible function in the physiology of the trees. Such speculations should, however, be preceded by ontogenetic and experimental studies.

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REFERENCES

BACK, E. L. (1969): Intercellular spaces along the ray parenchyma. The gas canal system of living wood? *Wood Science* **2** (1): 31–34.

ESAU, K. (1960): *Anatomy of Seed Plants*. London.

GODWIN, R. H. & D. R. GODDARD (1940): The oxygen consumption of isolated woody tissues. *Amer. J. Bot.* **27**: 234–237.

GREGUSS, P. (1955): *Xylotomische Bestimmung der heute lebenden Gymnospermen*. Budapest.

HARADA, H. & A. B. WARDROP (1960): Cell wall structure of ray parenchyma of a softwood (Cryptomeria japonica). *J. Jap. Wood Res. Soc. (Mokuzai Gakkaishi)*. **6** (1): 34–41.

International Association of Wood Anatomists. (1964): *Multilingual glossary of terms used in wood anatomy*. Winterthur.

JUTTE, S. M. & B. J. SPIT (1963): The submicroscopic structure of bordered pits on the radial walls of tracheids in parana pine, kauri and european spruce. *Holzforschung*. **17** (6): 168–175.

LAMING, P. B. (1972): Bijdrage tot het inzicht betreffende impregnering van Vuren (Picea abies); in het bijzonder van vloeistoftransport in radiale richting. *Report H-72-XVII, Houtinstituut TNO*.

MOLLER, C. M. & D. MÜLLER (1938): Aanding i aeldre Stammer. *Forstl. Forsoks v. Danm.* **15**: 113–138.

NYREN, V. & E. L. BACK (1960): Characteristics of parenchymatous cells and tracheidal ray cells in Picea abies Karst. The resin in parenchymatous cells and resin canals of Conifers. VI. *Svensk Papp. Tidn.* **63**: 501–509.

PANSHIN, A. J. & C. DE ZEEUW (1970): *Textbook of Wood Technology*. Vol. I, Ed. 3. New York.

REDIES, H. (1962): Ueber "homobare" und "heterobare" Interzellularsysteme in höheren Pflanzen. *Beitr. z. Biol. d. Pflanz.* **37** (3): 411–445.

REINDERS, E. & C. A. REINDERS-GOUWENTAK (1961): *Handleiding bij de plantenanatomie.* 5e dr. Wageningen.

RUSSOW, E. (1883): Zur Kenntnis des Holzes, insonderheit des Coniferenholzes. *Bot. Centralbl.* **13**: 134–144.

WARDROP, A. B. (1964): The structure and formation of the cell wall in xylem; in M. H. ZIMMERMAN: *The formation of wood in forest trees*. New York.