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WOOD AND BARK ANATOMY OF AZIMA TETRACANTHA LAM. (SALVADORACEAE) WITH DESCRIPTION OF ITS INCLUDED PHLOEM

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SUMMARY

The anatomy of the secondary phloem and xylem of the large shrub *Azima tetracantha* Lam. (Salvadoraceae) from Madagascar, has been studied. The presence of included (interxylary) secondary phloem, previously only known in the two other genera of this family, *Dobera* and *Salvadora*, has been demonstrated. The phloem strands in the secondary xylem belong to the foraminate or *Strychnos* type.

Sieve elements of the normal external secondary phloem are in contact with the vertical included secondary phloem strands by means of horizontally oriented ones within the wider rays. A three-dimensional network of sieve elements exists throughout the secondary stem tissue, interrupted by the cambial zone.

1. INTRODUCTION

The Salvadoraceae are a small family of trees and shrubs native to arid, often saline areas in Africa, Madagascar and tropical or subtropical Asia. The family is represented by three genera and 11–12 species (SLEUMER 1942), viz. *Azima* Lam. (four species), *Dobera* Juss. (two-three species) and *Salvadora* Garcin ex L. (five species). In KSHETRAPAL's (1970) opinion the Salvadoraceae may be divided into two subfamilies, the Azimoideae comprising *Azima* and the Salvadoroideae composed of *Dobera* and *Salvadora*. *Azima* is armed with axillary spines, the two other genera are unarmed. Included (interxylary) phloem is absent in *Azima*, present in *Dobera* and *Salvadora* according to SLEUMER (1942) and METCALFE & CHALK (1950). The relationships of the family are doubtful; it is now placed in the order Celastrales (TAKHTAJAN 1969; HUTCHINSON 1973). The family was placed within the Celastrales close to the Celastraceae by KSHETRAPAL (1970) based on evidence from floral structure, vascularization and embryology. GIBBS (1958) and LOBREAU (1969) on the other hand, using biochemical data and morphology of the pollen grain respectively, suggest relationship of the Salvadoraceae with the Aquifoliaceae.

2. MATERIALS AND METHODS

The bark and wood samples of *Azima tetracantha* Lam. used in this study, were collected by the authors (V & O nr. 1063) in Madagascar (1978), 18 km south of

Tulear near the coast at a height of 5 m above sea-level. The samples are housed at the Department of Botany, the accompaning herbarium vouchers at the Department of Plant Taxonomy and Plant Geography, both at Wageningen, The Netherlands.

The collected specimen is a large shrub of 4 m high, with a stem diameter of 10 cm. The stem sample was immediately fixed in F.A.A. All sections were embedded in Kaiser's gelatin-glycerin (JOHANSEN 1940). Means and ranges of the length of sieve-tube members, vessel members, parenchyma strands, radial vessel diameter and ray height are based on at least twenty-five individual measurements. The sieve-tube type, sieve-area type and companion-cell type were classified according to ZAHUR (1959).

3. RESULTS

3.1. Bark anatomy

The bark of *Azima tetracantha* Lam. is about 1660 µm thick. It can be divided into five zones (*plate 1, fig. 1*): the conducting secondary phloem (250 µm) immediately outside the cambial zone; the non-conducting secondary phloem (750 µm) divided into an inner part (190 µm) without fibre sclereids and an outer part (560 µm) composed almost entirely of fibre sclereids and near the pericycle zone also of some crushed primary phloem; the pericycle zone (90 µm) with fibre groups in tangential direction alternating with dilatating parenchyma cells; the cortical part (190 µm) consisting of dilatating parenchyma cells and some rather thick-walled stone cells; finally one periderm layer (300 µm).

The axial system of the conducting secondary phloem is composed of radial rows in which usually sieve tubes and companion cells alternate with parenchyma cells; also small groups of sieve tubes and companion cells occur. Storied structure present, rays excluded.

In the non-conducting secondary phloem the sieve tubes and companion cells collapse and towards the pericycle zone gradually more fibre sclereids differentiate out of parenchyma cells. These areas of the axial system are wedge-shaped, because the rays dilate according to the *Tilia* type.

Sieve-tube members oval to rectangular in cross section, in tangential direction 16 µm, in radial direction about 14 µm; short (type III), length (140–)165 (–190) µm. Sieve plates simple, slightly oblique to horizontal. Sieve areas in the side walls obscure or entirely absent (type III). *Companion cells* as long as the sieve-tube members they accompany (type B), tangential diameter 3 µm, usually situated along one of the radial walls of the sieve-tube member or in corners. *Parenchyma cells* in the conducting secondary phloem rectangular in cross section, in tangential direction 19 µm, in radial direction 6 µm; contents plasma; strands of two cells, or more often fusiform parenchyma cells, height (140–)165(–190) µm. *Rays* seldom uni-, often multiseriate without tails or with tails of only three cells high at a maximum; almost entirely composed of square or upright cells; (1–)10(–17)-seriate, average width 200 µm; height (380–)1400(–2900) µm; average number per tangential mm four. The central part of the wider rays is composed of rather thin-walled stone cells; only the outer one or two layers of these rays consist of parenchyma cells (*plate I, fig. 1*). These stone-cell plates protrude with the cambial zone somewhat into the secondary xylem. Scattered in the dilating rays of the non-conducting secondary phloem, rather thin-walled stone cells occur outside these stone-cell plates. Rays are often arranged close together in vertical rows as seen in tangential section, regularly forming aggregate rays. The longitudinally oriented elements of the axial system within such a vertical row are bent in a horizontal or almost horizontal direction between two rays, giving the impression of a transverse section in a radial view. *Crystals* rhomboidal, in stone cells of the rays.

3.2. Wood anatomy

Growth rings absent. Wood diffuse-porous. Storied structure present, rays excluded (*plate III, fig. 10*).

Vessels on average 30/mm^2, in radial multiples of two to four and in irregular clusters; round to slightly oval; radial diameter (25–)60(–95) µm. Vessel-member length (130–)150(–200) µm. Perforations simple in horizontal end walls; intervessel pits bordered, alternate, average horizontal diameter 3–4 µm; vessel-ray and vessel-parenchyma pits half-bordered, average diameter 4 µm. Vessels usually in contact with axial parenchyma, less often to seldom with libriform fibres and rays. Tyloses and deposits absent. *Fibres* libriform, non-septate, thick-walled; pits simple to slightly bordered, tending to be confined to the radial walls. *Parenchyma* abundant, in long, often concentric, (2–)7(–16)-seriate tangential bands, averaging three per radial mm; consisting of strands of two cells, or more often of fusiform cells, mean height 160 µm, in radial rows, rectangular to oval in cross section; also vasicentric and scantilly diffuse or diffuse-in-aggregates. In the outer part of the secondary xylem, vertical strands of less thick-walled cells are formed within approximately every seventh tangential parenchyma band; these strands are usually bordered by two adjacent rays; also tangential series of these strands occur (*plate I, figs. 1* and *2*). Ray-parenchyma cells in contact with these strands are thin-walled; even the whole ray part between two adjacent vertical strands, can be composed of thin-walled parenchyma cells (*plate I, figs. 2* and **3**). The central parts of these strands have differentiated into sieve tubes and companion cells (*plate I, fig. 4*). These strands are often on the outer as well as on the inner side bordered by cambium-like cells (*plate I, fig. 3*). In longitudinal direction these strands are very long (*plate III, fig. 10*). *Rays* seldom uni-, often multiseriate without tails or with tails of only three cells high at a maximum; almost entirely composed of square and upright cells; the procumbent cells are short in radial direction; (1–)10(–17)-seriate, average width 200 µm; height (380–)1400(–2900) µm; average number per tangential mm four. The central part of some multiseriate rays is composed of less thick-walled parenchyma cells. The middle areas of these long horizontally stretched parts, have also differentiated into sieve tubes and companion cells as in the longitudinal strands of included phloem embedded in the tangential axial-parenchyma bands (*plate III, figs. 9* and *12*). Rays are often arranged close together in vertical rows as seen in tangential section, regularly forming aggregate rays. The longitudinally orientated elements of the axial system are bent within such a vertical row in a horizontal or almost horizontal direction between two rays, as in the secondary phloem (*plate II, fig. 8*). *Crystals* rhomboidal, in ray-parenchyma cells.

The vertical thin-walled parenchyma strands occurring in a tangential layer in the secondary xylem with sieve elements in their centre are in mutual contact. Thus a network of included phloem strands exists within the different tangential zones of the secondary xylem (*plate III, fig. 11*). A connection in radial direction by means of vertical included phloem strands which are more or less oblique in the radial plane, has not been observed. This connection is achieved by included phloem strands within the wider xylem rays (*plate II, figs. 5, 6* and *7*). Vertically orientated sieve elements bend into a horizontal direction and join the sieve elements within the wider rays (*plate III, fig. 12*). In the conducting secondary phloem near the cambium these horizontally orientated phloem strands are wedge-shaped and divided by the central vertical stone-cell plates of the phloem rays (*plate I, fig. 1*). They soon bend into a vertical direction and become part of the normal external phloem. No sieve elements are present in the cambial zone.

Therefore, the cambium forms on its outer side normal external secondary phloem and on its inner side besides secondary xylem, locally, included phloem strands differentiated from thin-walled parenchyma cells in a vertical as well as in a horizontal direction. Both vertically orientated secondary phloem systems are connected with each other by way of the horizontally orientated phloem strands within the rays. Thus a three-dimensional network of sieve elements exists, interrupted by the cambial zone.

4. DISCUSSION

The description of the secondary xylem of *Salvadora persica* L. given by SINGH (1944), is not entirely in conformity with those of CHALK & CHATTAWAY (1937) and METCALFE & CHALK (1950). Based on material of both *Salvadora persica* L. and *Azima tetracantha* Lam. cultivated in Kew, METCALFE & CHALK's description includes for instance: vessels mostly in radial pore multiples of two to four (not two to eight as reported by SINGH 1944); wood fibres with simple pits, tending to be confined to the radial walls (not with bordered pits); rays composed of square and slightly procumbent cells (not of radially elongated cells).

Our observations generally correspond with those of CHALK & CHATTAWAY (1937) and METCALFE & CHALK (1950), although only *Azima tetracantha* Lam. has been studied. Differences are, for instance, the (1–)10(–17)-seriate rays, instead of three to five cells wide as reported by METCALFE & CHALK (1950). More important is the presence of included phloem, previously, reported only in the genera *Dobera* and *Salvadora*, but not in *Azima* (SLEUMER 1942; METCALFE & CHALK 1950; KSHETRAPAL 1970). The origin and development of the vertical included phloem strands in *Azima tetracantha* Lam. are very similar as in *Sal-*

vadora persica L., described by SINGH (1944), who does not mention, however, horizontal included phloem strands in the rays and therefore not a three-dimensional network of sieve elements either.

Two types of included phloem are distinguished in the IAWA glossary (1964):

- foraminate type (*Strychnos* type); a single permanent cambium continues to function throughout the life of the stem and the xylem is normal except for the occurrence of strands of phloem imbedded in it;
- concentric type (*Avicennia* type); the cambium is short-lived and is replaced by new meristimatic tissue, which develops in either the pericycle or the cortex and repeats the structure of the young stem; the stem thus consists of alternating zones of xylem and phloem.

The phloem strands or layers in *Azima tetracantha* Lam. like in *Salvadora persica* L. (SINGH 1944) belong to the foraminate type.

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Plate I. *Azima tetracantha* Lam. Transverse sections.

1. From top to bottom: periderm, cortex parenchyma, fibre groups of the pericycle, non-conducting and conducting secondary phloem with stone-cell plates in the wider rays, cambium which has just produced on its inner side a tangential zone of thin-walled parenchyma strands in which sieve elements are not yet or partly differentiated, normal secondary xylem, a tangential zone included phloem strands. In the centre of the figure a horizontally orientated included phloem strand within a wide ray.
2. A deeper section of the same sample as *fig. 1*, showing the secondary xylem just inside the cambium. Note the thin-walled parenchyma cells of the wood ray passing through two adjacent vertically orientated included phloem strands.
3. A vertical included phloem strand with some cambium-like cells on its outer as well as inner side.
4. A vertical included phloem strand bordering a wood ray on one side.

Plate II. *Azima tetracantha* Lam.

5. Radial section. From left to right: periderm, cortex parenchyma, secondary phloem, cambium, secondary xylem beginning with a vertical included phloem strand. This strand is in connection with two horizontally orientated phloem strands within rays. Note the stone-cell plates within the phloem ray.
6. Radial section of the secondary xylem. Connection of two horizontal phloem strands within rays with a vertical included phloem strand.
7. Detail of *fig. 6*.
8. Tangential section of the secondary xylem. Note the almost horizontally orientated vessel parts between rays.

Plate III. *Azima tetracantha* Lam. Tangential sections of the secondary xylem.

9. A vertical row of wood rays each containing a horizontally oriented included phloem strand.
10. A vertical included phloem strand between two rays. Note the storied structure of the axial elements.
11. Joining of two vertically orientated included phloem strands.
12. Connection between a vertical and a horizontal included phloem strand.

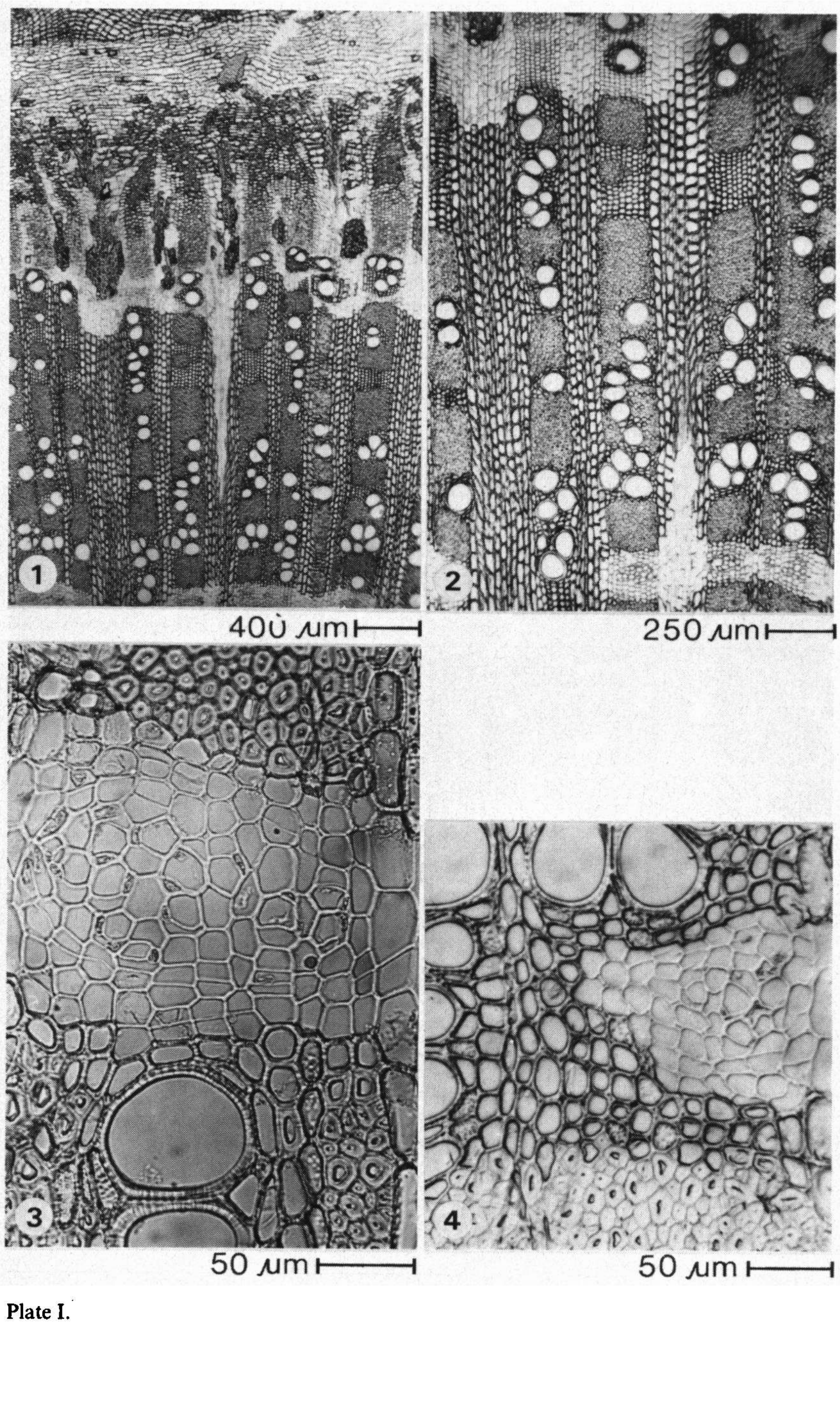

Plate I.

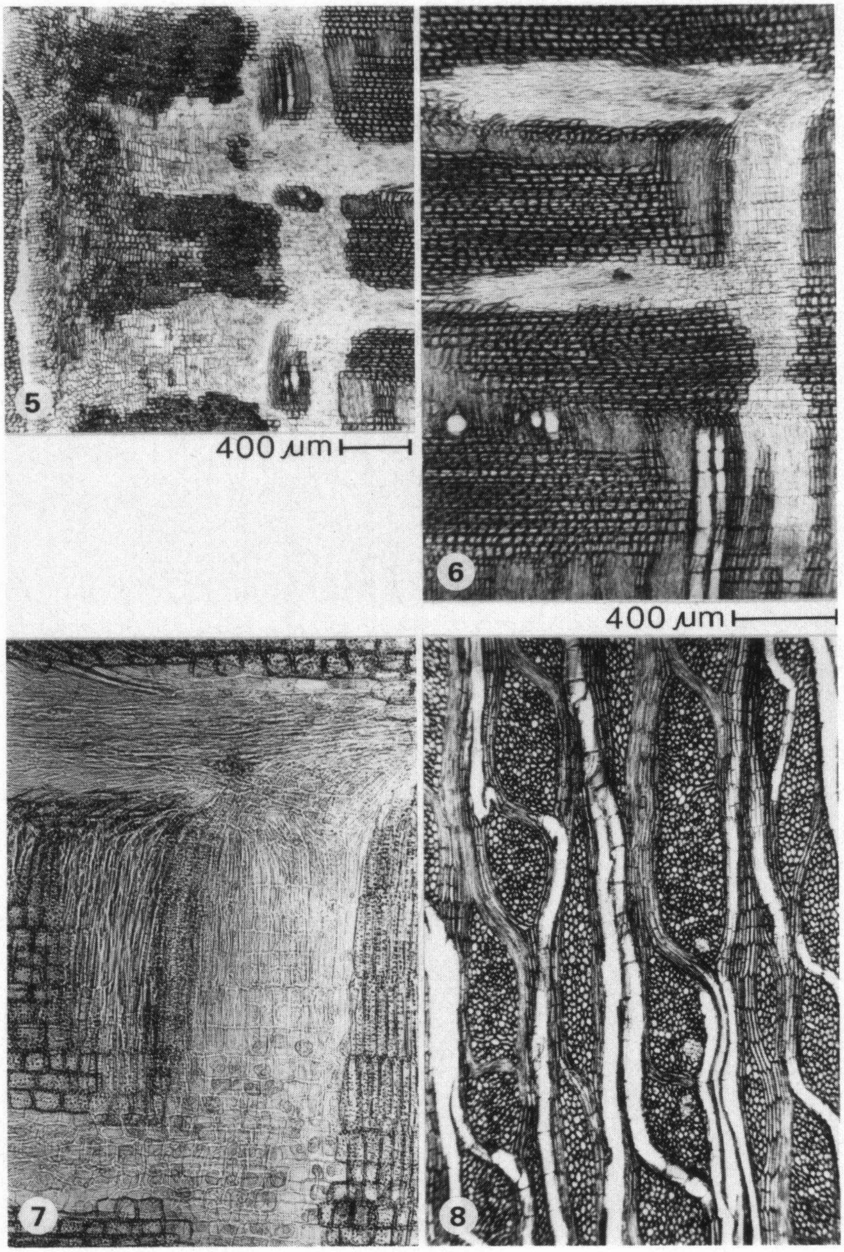

Plate II.

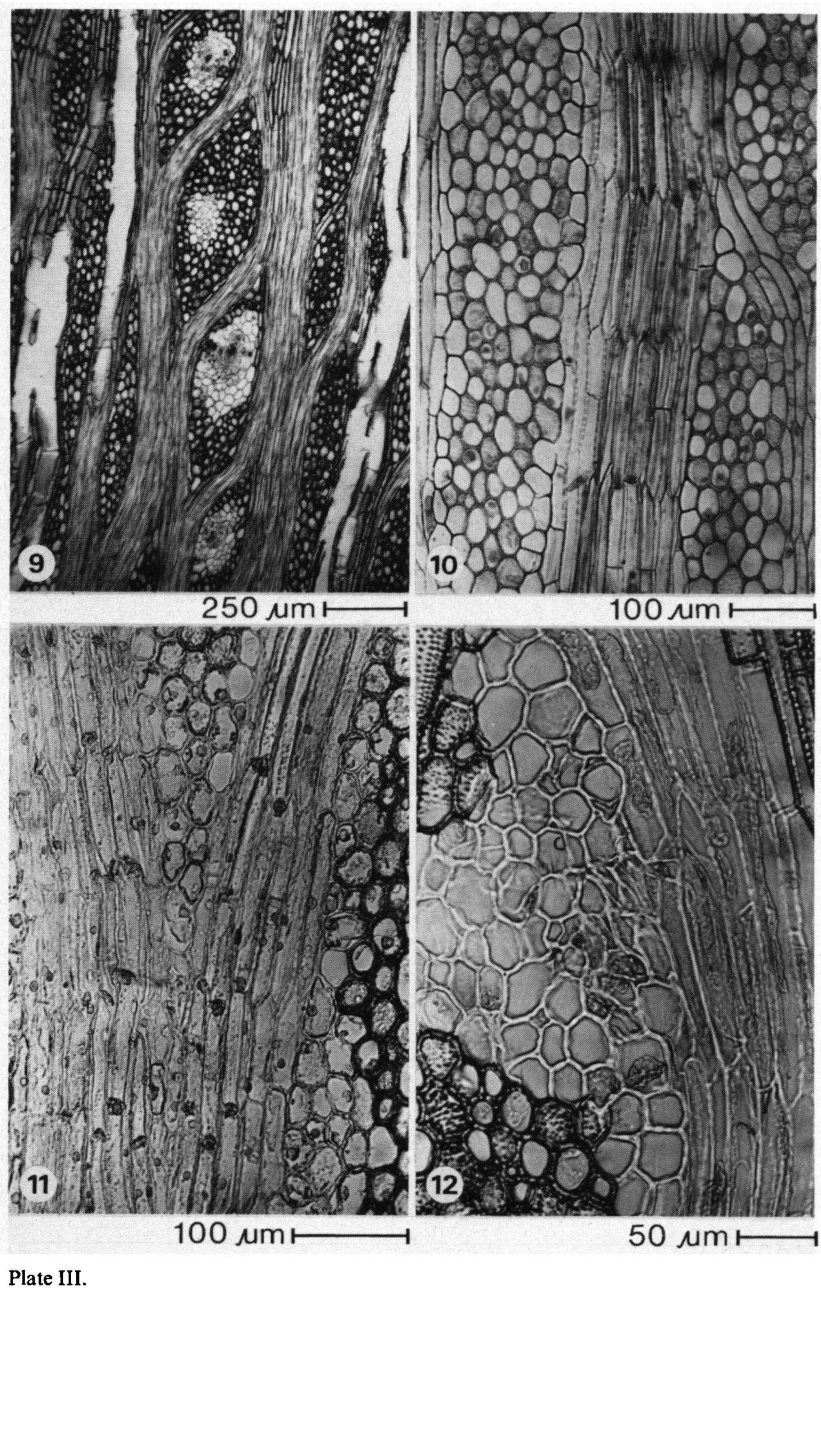

Plate III.