STUDIES ON FOLIAR SCLEREIDS IN DICOTYLEDONS

I. Structure and Ontogeny of Sclereids in the Leaf of Diospyros discolor Willd.

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INTRODUCTION

The importance of the study of foliar sclereids was recognised as far back as 1908 by Solereeder, who pointed out their possible taxonomic value. Recent studies by Bailey and Nast (1944, 1945), Foster (1944, 1945 a), Subramanyam and Rao (1949) have confirmed their taxonomic significance in differentiating species within the genus. More interest, however, is being centred now on the ontogenetic development of sclereids, and important contributions by Foster (1945 b, 1947), Bloch (1946), Sterling (1947) and others have considerably advanced our knowledge about them. Recently the writer (1951) made an attempt to classify sclereids into different groups, based upon their origin from the epidermis, palisade or spongy cells.

Statements on the terminal, subterminal or diffuse types of distribution of sclereids are usually based on observations made on mature sclereids in the leaf-tissue but it is only in a few cases that the early developmental stages have been studied. As pointed out by Foster (1946), the question whether the terminal sclereids originate from procambial cells in the developing veinlets or from adjacent cells of the ground meristem is of great interest. Recently, the finding of terminal as well as diffuse sclereids in the leaf of Diospyros discolor prompted me to make detailed observations on their origin and development.

MATERIALS AND METHODS

The material for study was collected at the Government Botanic Gardens, Bangalore. Diospyros discolor is a medium-sized tree with large oblong coriaceous leaves. It is a native of the Philippine islands. Vegetative buds as well as small portions of young and old laminae were fixed in formalin-acetic-alcohol. Microtome sections were stained by employing the tannic
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acid-iron chloride-safranin method (Foster, 1934). Leaves were cleared and macerated as suggested by Foster (1946) and permanent mounts were prepared by the method outlined by Subramanyam and Rao (1949).

Distribution of Sclereids in the Mature Lamina

As described by Solereder (1908) the mesophyll of the mature lamina has a single layer of palisade cells on the adaxial side and a moderately lacunate spongy parenchyma. The smaller as well as larger veins are accompanied by well-developed sclerenchymatous cells.

One of the most salient features of the cleared leaf is the occurrence of sclereids both diffuse as well as in contact with the end of the veinlets (Plate IV, A–D). The sclereids are abundantly present near the midrib region. Diffuse sclereids are more numerous than the sclereids in contact with the tracheary elements of the veinlets. Exceptionally all the veinlets in a large vein-islet may be in close contact with the sclereids (Plate IV, A). Occasionally a portion of the tracheary vein or sclerenchyma or both may incurve towards the diffuse sclereid (Plate IV, A).

The study of macerated material and transverse sections of the mature lamina reveal that the sclereids are short prop-like 'cell forms', distributed mostly in the palisade region and slightly protruding into the lacunar space (Figs. 12–13). The abaxial side of the sclereid, sometimes throws short branches extending into the lacunæ, whereas the adaxial side abuts close to the epidermal cells without undergoing any branching. On the whole, the sclereids do not show much variation in their shape, but differ slightly from each other in the possession of arrested plug-like branches at the abaxial tip. In no instance do the mature sclereids extend up and down so as to touch the two epidermal layers. Such form types are seen in the laminae of Linociera macrophylla Wall, and L. intermedia Wight (Rao, 1950). In rare cases, on the adaxial side the mature sclereids slightly protrude between the radial epidermal walls and sometimes may even extend beyond them into the cuticle. Such a feature is reported in Mouriria huberi Cogn. (Foster, 1947).

Ontogeny

Developmental stages of the sclereids were traced in sections of young leaves taken from unfolding leaf-buds. In early stages the young lamina consists of 5 to 9 layers of closely arranged cells with small intercellular spaces. The vascular bundles are in an active state of differentiation, and a sheath of polyhedral cells is soon seen surrounding the xylem and phloem. The cutinised epidermis is clearly demarcated on the adaxial surface. At this stage the sclereid initials appear as large polyhedral cells, differ from
the adjacent cells by their slightly larger size, vacuolated cytoplasm and a prominent nucleus (Figs. 1–3). Such features have also been reported in *Mouriria huberi* (Foster, 1947). A careful examination of the lamina reveals that the sclereid initials originate from the cells of third layer situated beneath the upper epidermis. In the sub-marginal region they are in intimate contact with the differentiating vascular bundles. There was no evidence for a differentiation of the sclereid initials at the terminal portions of the procambial strand as reported in *Mouriria huberi* (Foster, 1947) and *Memecylon heyneanum* (Rao, in press). They are situated just above and outside the sheath of the vascular bundle. The enlargement of the sclereid initial is independent of the vascular differentiations in spite of its seemingly close contact with the vascular bundle in later stages. This reveals that the sclereid initial cell is a transformed spongy cell and not an integral part of the veinlet end.

In the course of development, the sclereid initial cells which are at first sub-spherical to polygonal in outline show a tendency to elongated in the vertical direction of the leaf. They may also throw small adaxial and abaxial processes (Figs. 5–6). These plug-like processes extend intercellularly between the walls of neighbouring cells. They make their way mostly in a vertical direction and very rarely in an oblique direction. The adaxial part of the growing sclereids enters the palisade region, which is well differentiated with a well-developed epidermal cells. Meanwhile the abaxial part grows downwards between the cells of the spongy parenchyma coming to a stop as it enters an air-lacuna (Fig. 7). The adaxial end of the sclereid does not show any branching. Only rarely small tube-like processes may extend between the walls of epidermal cells (Fig. 10). The abaxial end may, however, show slender dichotomous or trichotomous processes extending into the intercellular spaces (Figs. 8–9). In the final stage the abaxial processes do not fill up the intercellular space but they occupy a portion of the moderately big air lacuna. Such a feature is reported in the petiolar sclereids of *Camellia* (Foster, 1944). As in *Camellia, Trochodendron, Mouriria huberi* (Foster, 1944, 1945 b, 1947), *Ternstroemia japonica* (Rao, in press) and *Olea* (Rao and Kulkarni, 1951) the sclereids of *Diospyros discolor* remain uninucleate although the nucleus may occupy different positions in the enlarging cell. In the final stage the sclereids develop a massive lignified wall leaving only a narrow lumen. The wall is homogeneous and possesses slender pit canals, which are often branched or forked as in *Camellia* (Fig. 11). The degenerating nucleus can be observed up to a late stage of lignification of the sclereid.
Figs. 7–13
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SUMMARY

The sclereids in the cleared mature leaf of Diospyros discolor show two types of distribution with reference to veinlets; either terminal or diffuse. Ontogenetic studies have, however, revealed that the initials of the seemingly terminal sclereids arise away from the procambial strands. They are in fact transformed cells of the spongy parenchyma and the terminal appearance is due to juxtaposed development. Sclereids should not be designated as "terminal" merely on the basis of their position in the mature leaf unless this is compared by an ontogenetic study.

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EXPLANATION OF FIGURES

FIGS. 1–7. Transections through the submarginal portions of young laminae showing early stages in sclereid ontogeny × 450 each.

FIG. 1. Very young sclereid initial cell in close contact with differentiating veinlet.

FIG. 2. Sclereid initial cell showing adaxial and abaxial processes.

FIG. 3. Idioblastic sclereid initial cell along with the sclereid initial cells in contact with the differentiating veinlet. Note the irregular shape and sharp processes of idioblastic sclereids.

FIGS. 4–7. Sclereid initial cells of the expanded lamina of immature leaves, showing the prominent growth processes on the adaxial and abaxial sides.

FIGS. 8–11. Transverse sections of nearly mature lamina showing advance stages in sclerid ontogeny × 450 each.

FIG. 8. Adult sclereid in close contact with the veinlets showing broad lumen and protoplast and nucleus.

FIG. 9. Adult diffuse sclereid with forked abaxial process lying in a small air space.

FIG. 10. Near the margin — Adult pseudo-terminal sclereid.

FIG. 11. Adult idioblastic sclereid with channel-like lumen and forked pit canals.

FIGS. 12–13. Transections of mature lamina showing pseudo-terminal & idioblastic sclereids. Note the branched or unbranched abaxial processes occupying a small portion of the air-lacuna.

A to D — Cleared lamina of Diospyros discolor showing the occurrence of diffuse sclereids as well as sclereids in contact with the end of veinlets, × 100 each.