ROOT SCLEREIDS OF *SYZYGIUM CUMINI* (L.) SKEELS

By A. R. RAO* AND C. K. RAO

(*Department of Botany, Bangalore University, Bangalore*-1)

Received September 29, 1971

(Communicated by Professor L. Narayana Rao, F.A.SC.)

ABSTRACT

Sclereids in the roots of *Syzygium cumini* (L.) Skeels (Myrtaceae) are polymorphic. In addition to the brachy-, osteo- and bizarre sclereids, there occur an interesting kind of sclereids—the fibre sclereids—resembling the fibres in some respects.

Sclereids appear only after the onset of secondary activity and fall into one of the following categories depending on their origin: (*a*) a continuous strand of sclereids in the secondary cortex. This develops from parenchymatous initials that are derivatives of phellogen. Fibre sclereids occur only in this region along with ordinary sclereids and a few fibres. (*b*) sclereids formed through secondary sclerosis of distal mature parenchyma cells of the dilating phloem rays. (*c*) Sclereids formed through secondary sclerosis of mature parenchyma cells in old phloem. Sclereids of categories *b* and *c* abut on those of *a* forming a composite strand.

All the kinds of sclereids here possess thick, highly lamellated lignified walls with simple and wide pit canals ending in round or oval apertures. The adult sclereids are devoid of nuclei, starch or crystals. Insoluble tannin is present in them except in those formed from phloem parenchyma.

Ontogenetical stages of the various kinds of sclereids are similar except that fibre sclereids show a pronounced intrusive growth which although initially bipolar later becomes unipolar. Other kinds of sclereids show either a purely symplastic growth or a combination of various degrees of symplastic and intrusive growth which is either diffuse (some osteosclereids) or multipolar (bizarre sclereids).

The inadequacy and unreliability of the existing classifications of and criteria for classifying different mechanical elements particularly in sclereid containing plants are discussed and suggestions made.

* Present address: No. 2, XI Main Road, 3rd Block East, Jayanagar, Bangalore-11.

INTRODUCTION

THE sclereids in the aerial parts of a number of gymnosperms and angiosperms were studied in considerable detail while scant attention was paid to the sclereids in their roots although the occurrence of sclerosed cells under different names has no doubt been recorded in the roots of some plants (Metcalfe and Chalk, 1950). Neither were these cells recognized as sclereids nor was any attention paid to the details of their structure and ontogeny. The sclereids in the roots of *Nymphaea mexicana* (Cutter, 1969) have been described in some detail. Sclereids in the roots of *Gnetum ula* Brongn. were studied by us (Rao and Rao, 1971). They differ from the sclereids in the aerial parts in several respects. Pursuing the same line of study, the distribution, structure and ontogeny of sclereids in the underground roots of the Myrtaceous angiosperm *Syzygium cumini* (L.) Skeels were investigated and the results are presented in this paper. The sclereids of the stems and fruits of this species and of *S. nodosum* Miq., *S. cinereum* Wall., and *Eucalyptus tereticornis* Sm. Austral., were studied by Malaviya (1967), who found that the leaves of all these species were devoid of sclereids.

Lignified mechanical elements were reported from the cortex of the adventitious roots of *Melaleuca linarifolia* Sm., (Musson and Crane, 1910) and the climbing roots of *Metrosideros hypericifolia* A. Cunn., (Bird, 1915). With the exception of these two species. roots of no other Myrtaceous plants investigated from this point of view are known to us. Even in these, details of structure and ontogeny of the mechanical elements are unavailable. From the descriptions, these cells may be presumed as sclereids developed through secondary sclerosis of the chlorenchymatous cells of the secondary cortex in the climbing roots of *Metrosideros hypericifolia*.

MATERIALS AND METHODS

Roots of different ages of *Syzygium cumini* (L.) Skeels were obtained from the trees growing on the Bangalore University's Central College Campus. Usual methods of staining and maceration were employed (Foster, 1949; Sass, 1958). Tannin was tested for in fresh sections using ferric chloride (Jensen, 1962).

OBSERVATIONS

Distribution

The primary cortex does not show any sclereids. In older roots sclereids are found in the secodnary cortex in the form of a continuous strand of

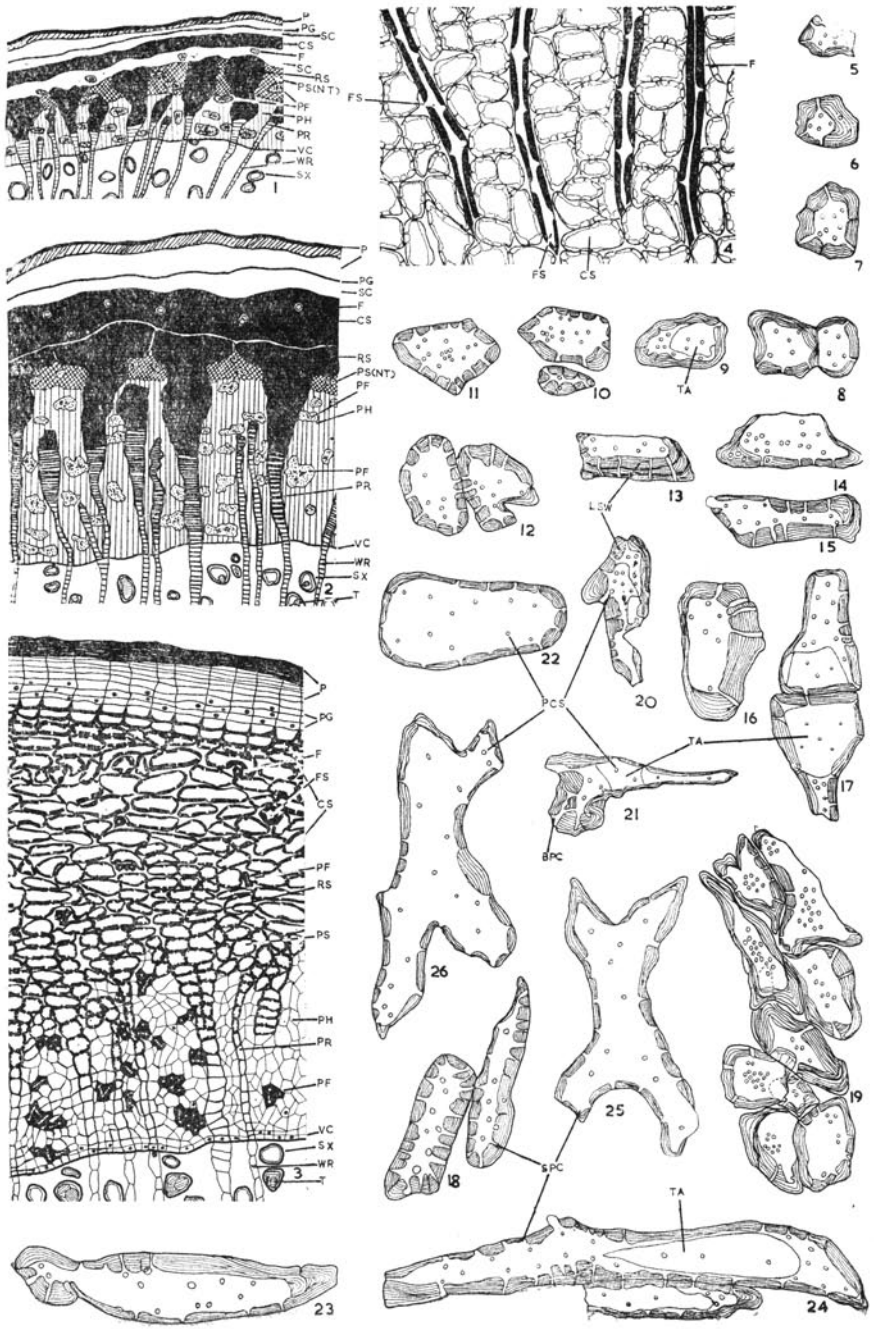
about 8–16 sclereids in thickness (Figs. 2, 3). This is a composite strand consisting of sclereids formed in the secondary cortex itself, sclereids formed from the distal cells of the phloem rays and sclereids formed from parenchyma cells in the old phloem. In stages younger than this, a few layers of parenchyma separate for a time, the strand of sclereids in the secondary cortex and the sclereids developing from the phloem rays and phloem parnchyma (Fig. 1). Anticlinal divisions occur in several parenchymatous cells of the phloem rays prior to their differentiation into sclereids. As a result, the phloem ray sclereids are two to four cells wide in a tangential series as observed in transections (Fig. 3). The rays assume a dilated appearance as the cell or cells of the outermost tangential series being the widest (Figs. 1, 2, 3). The width of the rays decreases gradually towards the vascular, cambium (Figs 1, 2, 3). Whether sclereids or parenchyma cells. all the cells of the ray contain tannin like the sclereids in the secondary cortex whereas the phloem sclereids are usually devoid of tannin.

In the earlier stages, though the phloem ray sclereids and phloem sclereids abut on the (4–8 sclereid thick) strand of sclereids in the secondary cortex, they can be distinguished from each other. In older roots, however, they merge with each other and the identity is obscured (Fig. 3). Consequently, the entire strand is a composite one, about 8–16 sclereids in thickness. By this time, the secondary xylem vessels show plenty of tyloses (Figs. 2, 3).

Structure

Osteosclereids (*sensu* Tschirch, 1889) predominate in this material. Although the bulk of the sclereids are either osteo or brachysclereids (Figs. 5–24), a few bizarre sclereids also occur (Figs. 25, 26). All these kinds of sclereids which are of highly varying sizes, have lignified secondary walls of varying thickness. The walls are highly lamellated, irregularly thickened and are traversed by simple but wide pit canals. Occasionally, branched pit canals also are seen (Fig. 21). In some isolated sclereids sharply delimited thin broad areas in the wall, different from the adjoining parts are noticed (Figs. 9, 17, 20, 21, 24). These are the faces of contact between these sclereids and the neighbouring sclereids or parenchyma cells.

Associated with the various kinds of sclereids mentioned, occur certain other elements resembling the lignified fibres in several respects. These elements occur along with the ordinary sclereids in the secondary cortex (Fig. 3) and are disposed parallel to the long axis of the root or obliquely to it (Fig. 4). These are regarded by us as sclereids for reasons detailed


P
PG
SC
CS
F
RS
PS(NT)
PF
PH
PR
VC
WR
SX
T
FS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
LSW
TA
PCS
BPC
SPC

FIGS. 1-26

further on and are designated as "fibre scle eids" (Figs. 32, 33) (Esau, 1965). Lignified fibres occur isolated or in groups of 2–6, mainly in the secondary xylem and secondary phloem (Figs. 1, 2, 3). A few lignified fibres, singly or in groups, occur also in the secondary cortex as well, along with the ordinary sclereids and the fibre sclereids (Figs. 2, 3, 4).

Like the ordinary sclereids, the fibre sclereids too possess lignified highly lamellated and irregularly thickened secondary walls traversed by wide and simple pit canals (Figs. 4. 32, 33). The true fibres also have lignified, sometimes fairly lamellated but usually *uniformly thickened* secondary walls (Figs. 27, 28). The pit canals in the true fibres could not normally be made out under the light microscope. However, in several fibres a few simple pit canals were noticed (Figs. 4, 28). In many instances, the two ends of the pit canals which are more or less slit-like, criss cross. The lumena as well as the pit canals in the true fibres are normally very narrow (Figs. 4, 27, 28). But in the fibre sclereids the lumena as well as the pit canals are wide and the apertures which are round or oval do not criss cross (Figs. 4, 32, 33). However, our observations indicate that these criteria are often inadequate to distinguish a fibre from a fibre sclereid. Indeed, there are certain elements (Figs. 29, 30, 31) which show a combination of fibre and fibre sclereid characters. In fact, an almost continuous spectrum from a true brachysclereid to osteo– and bizarre sclereids to fibre sclereids and then to true fibres has been noticed in this material. The differences and resemblances between the ordinary sclereids, fibre sclereids and the true fibres are shown in Table I. This table shows that not one or two characters but a combinations of characters (as presented in the table) should be relied upon for distinguishing one from the other. Interestingly enough, all the three categories of elements respond in the same way to staining tests with phloroglucinol or chlor-zinc-iodide. The fibre sclereids are normally larger in diameter than the true fibres which are two to four times longer than the fibre sclereids. The fibres are sometimes forked at one or both ends.

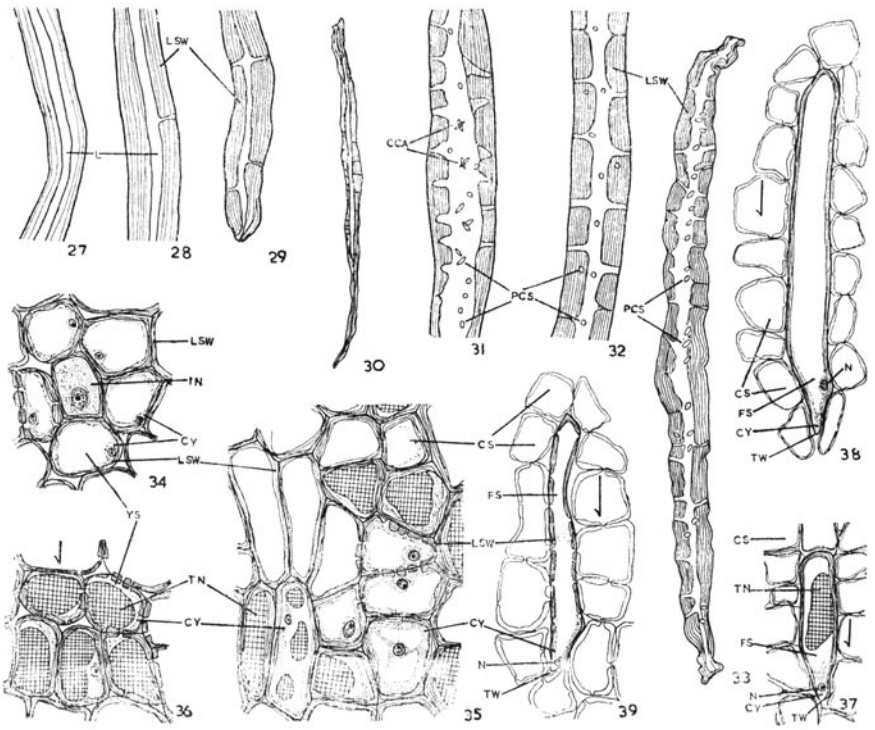
Tannin is normally present in all kinds of sclereids, except those formed from phloem parenchyma. Very young sclereids are often devoid of tannin (Figs. 34, 35). Tannin is often found in the fibre sclereids while in true fibres it is absent irrespective of their position. Older sclereids contain tannin that is usually nearly black in colour whereas in the young ones tannin is of a reddish or blackish-brown colour. The tannin present in this species is of the insoluble type and answers readily to the test with ferric chloride giving a blue precipitate in fresh material. The sclereids studied here so

TABLE 1

Structural and ontogenetic differences and resemblances between ordinary sclereids, fibre sclereids and fibres occurring in the root of Syzygium *cumini* (L.) Skeels

Particulars	Ordinary sclereids	Fibre sclereids	Fibres
Distribution	(i) Secondary cortex (ii) Phloem rays (iii) Old phloem	(i) Secondary cortex	(i) Secondary cortex (ii) Secondary phloem (iii) Secondary xylem
Sources and mode of differentiation	(i) Parenchymatous initials derived from phellogen (ii) *Mature distal cells of parenchymatous rays (iii) *Mature parenchymatous cellls of old phloem *differentiation through secondary sclerosis		(ii) Initials derived from vascular cambium
Mode of growth	Symplastic or a combination of varying degrees of symplastic and intrusive growth. Either diffuse (Osteosclereids) or multipolar bizarre sclereids)	Mostly intrusive.	Bipolar to start with and subsequently tends to be unipolar
Size	Highly variable	Diameters larger than those of the fibres	Two to four times longer than the fibre sclereids
Lumena	Very wide	Wider than in fibres	Very narrow
Pit canals	Numerous, wide and simple with wide round or oval apertures	Few, rather wide and simple with round or oval apertures	Normally observable only under polarizing light. In some few and narrow with slit-like criss. crossing apertures
Wall	Lignified Always highly lamellated, unevenly thick	Lignified	Lignified Occasionally well lamellated. Very thick and uniform
Contents	Insoluble tannin except in the phloem sclereids	Tannin occasionally present	Tannin usuallsy absent
Staining reaction	Lignin red to violet with phloroglucinol in hydrochloric acid Lignin yellow and cellulose blue with chlor-zinc-iodide		

far are devoid of any crystals. Mature sclereids show neither nuclei nor any cell contents other than tannin.



FIGS. 27–39.

Ontogeny

Ordinary sclereids :—These originate in groups or occasionally singly from parenchymatous initials in the secondary cortex. The initials are derived from the products of phellogen. There are two other sources of the ordinary sclereids: the distal mature parenchyma cells of the phloem rays and the mature parenchyma cells of the old phloem. In both these cases, differentiation of sclereids is through secondary sclerosis of mature parenchyma cells.

The cells that can be identified as sclereid initials are uninucleate and possess a larger nucleus and denser cytoplasm (Fig. 34) than the neighbouring parenchyma cells. Starch (not shown in figures) is sometimes found in the initials as well as in other parenchyma cells of the cortex. A shrinkage of the cytoplasm into a peripheral layer follows (Figs. 34, 35, 36). A rapid

depletion of starch when present in these initials is noticeable. Soon the whole protoplast gradually disappears and soon after further growth ceases. Simultaneously layer after layer of the wall substances are deposited (Figs. 34, 35, 36). Pit canals make their appearance after a several layers thick wall is built up. The initial lamellations are of lignin as evidenced by a positive staining reaction with phloroglucinol in hydrochloric acid. Accumulation of tannin starts long before the protoplast dies away (Figs. 35, 36). All sclereid initials show symplastic growth initially. Those that undergo only symplastic growth althrough develop into brachysclereids, while a combination of various degrees of symplastic and intrusive growth will produce the osteo- or bizarre sclereids.

As already mentioned, sclereids in the phloem rays and the old phloem develop from mature parenchyma cells. These are uninucleate and cannot be identified as initials on any ground prior to the onset of differentiation into sclereids. Details of ontogeny of sclereids developing from these cells are essentially the same as those that develop from initials in the secondary cortex except that the parenchyma cells in the phloem rays and phloem parenchyma are vacuolated with less cytoplasm unlike the initials with dense cytoplasm. We have noticed only brachysclereids in the phloem rays whereas both brachy- and osteosclereids are present in the old phloem. The secondary cortex contains all the three kinds of sclereids.

Fibre sclereids :—The fibre sclereids offer, but a few, variations in their ontogeny. As is well known the true fibres occurring in the secondary xylem and secondary phloem develop from the derivatives of the vascular cambium. But the true fibres as well as the fibre sclereids occurring in the secondary cortex along with the ordinary sclereids originate from initials derived from the products of phellogen which are also the source of the ordinary sclereids in this region. Growth in the fibre sclereids is exclusively intrusive as is the case with the true fibres. As in the true fibres, the fibre sclereids also show bipolar growth at first which later tends to become unipolar, that end of the initial towards the base of the root maturing earlier (Figs. 37, 38, 39). This point can be made out by the presence of a thinner wall at the growing end which also contains cytoplasm and nucleus as shown in the figures cited. This growing end is always the one pointing to the apex of the root. Until a very late stage in the ontogeny it is not always easy to determine whether a particular initial in development will result in a true fibre or a fibre sclereid. We believe that Fig. 37 shows a developing fibre sclereid in a tangential section. The presence of tannin is not a character of true fibres. Figures 38 and 39 are also from tangential sections through the secondary cortex

showing two stages in the ontogeny of the fibre sclereids (note the pit canals in Fig. 39). Except for the differences detailed here, other ontogenetical stages of the fibre sclereids are the same as those of the ordinary sclereids.

Discussion

The sclereids in the roots of *S. cumini* (L.) Skeels are mostly either osteo- or brachysclereids (*sensu* Tschirch, 1889) although a few bizarre sclereids also are present. In addition to these, some sclereids resembling fibres in some respects occur in the secondary cortex along with the ordinary sclereids and a few fibres. These are regarded as "fibre sclereids" following Esau (1965) as "it is difficult to assign" this kind of "sclerenchyma cells to one or the other category" of sclereids and fibres. Malaviya (1967) found only brachysclereids in the stems of this species while the fruits contained brachy-, osteo- and asterosclereids. Fibre sclereids were not found in the aerial parts. Sclereids were absent not only from the leaves of Syzygium but also in *Eucalyptus tereticornis*.

Both in the stems (Malaviya, 1967) and the roots of *S. cumini* sclereids appear only after the initiation of the activity of the vascular cambium. A similar observation was made in the roots of *Gnetum ula* (Rao and Rao, 1971). Sclereids are found in the pith and the cortex of the stems of *S. cumini* whereas they are present only in the secondary phloem and the secondary cortex of the roots, where there is no pith identifiable as such.

The sclereids assume the form of a continuous, 8–16 sclereid thick composite strand in the older roots. The phloem rays appear to abut on this strand of sclereids. Judging from their origin this strand consists of sclereids derived from three sources, *i.e.*, initials in the secondary cortex, mature parenchyma cells in the phloem rays and phloem parenchyma. Though sclereids from these sources were distinct initially, in old roots they merge with each other. In contrast to the situation in the roots, sclereids occur in groups of two to many in the stem cortex (Malaviya, 1967).

In cylindrical organs, almost always, sclereids develop in tissues that are in close proximity to the surface (Sinnott and Bloch, 1946; Rao and Rao, 1971). Although this is generally true in the roots of *S. cumini* in some instances, the phloem ray sclereids differentiate earlier than those of the secondary cortex.

The production of various kinds of sclereids in different zones in the root is a continuous process in the life of the plant as phellogen is repeatedly

disorganized and renewed. During this process the old sclereids, sometimes including those in the phloem zone, are discarded.

All the sclereids occurring in the roots are non-crystalliferous. They do not contain nuclei or cytoplasm or starch when mature. No crystals have been found in the stem sclereids of *S. cumini* or other species of Syzygium studied but one or two crystals were noticed in some stem sclereids of *Eucalyptus tereticornis* (Malaviya, 1967). In the roots of *S. cumini*, only the phloem sclereids are totally devoid of tannin. The remaining sclereids contain insoluble tannin. Since the parenchyma cells of the phloem rays which are tanniniferous differentiate into sclereids, sometimes undergoing a few anticlinal divisions, the tannin may be considered to be of the non-toxic kind. So far as we are aware, no information is available on the presence or absence of tannin in the sclereids of stems and fruits of the other Myrtaceous plants studied.

An interesting aspect of the roots of *S. cumini* is the occurrence of the fibre sclereids in the secondary cortex along with other types of sclereids and a few fibres. These fibre sclereids intergrade with the fibres on one hand and some of the much elongated osteosclereids on the other. They stand in between the true fibres and the ordinary sclereids. Sclereids occurring as component parts of xylem and phloem are known to intergrade with the fibres (Easu, 1965). The sclereids developing from the products of phellogen in the roots of *S. cumini* develop mostly into barchy- or sometimes osteosclereids. The development of the fibre sclereids from the derivatives of phellogen appears to be rather unusual.

Another point of interest is that the gamut of sclereids met with here includes an almost continuous spectrum ranging from brachysclereids to true fibres with the other kinds of sclereids falling in between, making it often difficult to distinguish a particular element. This makes the sclereid complement of the root highly polymorphic unlike that of the stem. Phellogen is the ultimate source for the ordinary sclereids, fibre sclereids and the fibres occurring in the secondary cortex, whereas vascular cambium is the ultimate source for the phloem ray and phloem sclereids and the xylem and phloem fibres. The fact that both fibres and sclereids can develop from products of either vascular cambium or phellogen minimises the fundamental difference between fibres and sclereids. As far as the roots of *S. cumini* are concerned all the elements referred to occurring in the secondary cortex develop from cells that can be identified as initials appearing in the ground tissue produced by the phellogen while the phloem ray sclereids and phloem sclereids develop

from mature parenchyma cells through secondary sclerosis. The parenchyma cells which are the products of the vascular cambium cannot be identified on any features as sclereid initials, prior to the onset of their differentiation into sclereids. The cortical sclereids in the Myrtaceous plants studied develop from initials in the cortex derived through the activity of phellogen.

In the stems of *S. cumini*, *S. nodosum* and *S. cinereum*, sclereid initials were found to be initially binucleate (Malaviya, 1967). In the roots we found only uninucleate initials which is also the case in the aerial parts of *Eucalyptus tereticornis*. A comparative study of the ontogeny of various kinds of sclereids in the roots of *S. cumini* shows that the brachysclereids are the result of purely symplastic growth. A combination of various degrees of symplastic as well as intrusive growth produces the osteo- and bizarre sclereids. In these, a pronounced polarity, as present in the fibre sclereids, is absent and therefore, growth should be considered as either more or less diffuse as in the osterosclereids or multipolar as in the bizarresclereids. On the other hand, purely intrusive growth builds up the fibres and the fibre sclereids. In these elements, growth is symplastic in the earliest stages. Subsequently intrusive growth sets in. During later stages of development growth is bipolar. However, as in the case of the true fibres, in the fibre sclereids too that end of the initial towards the base of the root matures earlier than the one towards the apex of the root, thus rendering growth unipolar. Such a close similarity between fibres and fibre sclereids is brought into focus when we see that it is difficult to say whether a particular initial in the secondary cortex develops into a fibre or a fibre sclereid. Our experience shows that there is but a very thin distinction between these elements. In fact, the conventional differences, structural or otherwise, between them do not help in clearly distinguishing one from the other. It is significant that the same degree of unreliability prevails in the generally accepted classification of sclereids it self, when we study the variations of form and structure and the intergrading of all the diverse kinds of sclereids into one another. This suggests that the existing classifications of sclereids and the criteria adopted need to be revised although Rao, T. A. (1957) has attempted and recognized on the basis of morphological data six main types of compact sclereid forms of wide occurrence in seed plants. These are spheroidal sclereids, osteosclereids, fusiform sclereids, filiform sclereids, astrosclereids and crystalliferous sclereids.

According to Rao, T. A. (1964) sclereids stand in comparison with fibres but differ from them in not forming a reticulum or compact strand.

However, sclereids form a compact strand in the roots of *G. ula* (Rao and Rao, 1971) and also of *S. cumini*.

Rodin (1963) could outline certain characteristic features of sclereids in the cone scales of *Welwitschia mirabilis*. He still felt it difficult to distinguish fibres from elongated sclereids. However, in Welwitschia lignification of the fibres cannot be detected with phloroglucinol in hydrochloric acid—presumably only cellulose is present in the fibres as in the fibres occurring in the roots of *G. ula* (Rao and Rao, 1971). In *S. cumini* even this criterion cannot be applied as all the mechanical elements respond in the same way to staining tests. Like the value of differences in the ulitmate sources of fibres and fibre sclereids in diagnosis, the criterion of pit canals also is unsatisfactory. Pit canals cannot usually be observed in the fibres under a light microscope. The fibres in the root of *S. cumini* often show easily observable pit canals. On the other hand the foliar sclereids in *G. ula* have pit canals that need the aid of a polarizing microscope to be resolved properly (Rao, T. A., 1965).

While we are not clear as to the factors determining the patterns of differentiation and ultimate form of different mechanical elements such as sclereids, fibre sclereids and fibres, the whole series of mechanical tissues described in this material appears to belong to rather a single category. Perhaps no natural classification of any practical value can be outlined taking one or two characters into consideration for all the kinds of mechanical tissues in plants in general. Nevertheless, a combination of criteria, structural and ontogenetic, may profitably be used to classify and identify the different components of mechanical tissue in plants as has been attempted by us for the roots of *S. cumini* (Table I). An attempt to arrive at a rational classification of various mechanical elements especially in sclereid-containing plants seems to be a desideratum. The use of an electron microscope and the scanning electron microscope would be highly rewarding and may even open a new area of study.

ACKNOWLEDGEMENTS

We are highly indebted to Professor M. Nagaraj, Head of the Department of Botany, Bangalore University, for giving laboratory facilities and encouragement.

References

*Bird, J. W. .. *Trans. N. Zealand Inst.*, 1915, **48**, 315.

Cutter, E. G. .. *Plant Anatomy: Experiment and Interpretation Part I. Cells and Tissues*, Edward Arnold (Publ.), Ltd., London, 1969.

Esau, K. .. *Plant Anatomy*, 2nd Ed., John Wiley and Sons, Inc., New York, 1965.

Foster, A. S. .. *Practical Plant Anatomy*, 2nd Ed., D. Van Nostrand Company, Inc., Princeton, 1949.

Jensen, W. A. .. *Botanical Histochemistry*, W. H. Freeman and Company, San Francisco, 1962.

Malaviya, M. .. *Proc. Ind. Acad. Sci.*, 1967, **66 B**, 45.

Metcalfe, C. R. and Chalk, L. *Anatomy of the Dicotyledons*, Vols. 1 & 2, Oxford Univ. Press, 1950.

Musson, C. T. and Crane, W. M. *Proc. Linn. Soc. N.S.W.*, 1910, **35**, 662.

Rao, A. R. and Rao, C. K. .. *Proc. Indian Sci. Congr.*, 58th session, Section VI: Botany, 1971, p. 433.

Rao, T. A. .. *Proc. Nat. Inst. Sci., India*, 1957, **23 B**, 152.

———— .. *Proc. Ind. Acad. Sci.*, 1964, **60 B**, 66.

———— .. *Ibid*,. 1965, **61 B**, 196.

Rodin, R. J. .. *American J. Bot.*, 1963, **50**, 641.

Sass, J. E. .. *Botanical Microtechnique*, 3rd Ed., Oxford and I.B.H. Publ. Co., Calcutta, 1958.

Sinnott, E. W. and Bloch, R. .. *American J. Bot.*, 1946, **33**, 587.

Tschirch, A. .. *Angewandte Pflanzenanatomie*, Wien and Leipzig, 1889.

* Not seen in original.

Explanation of Figures

BPC = branched pit canals; CCA = criss crossed apertures; CS = cortical sclereid strand; CY = cytoplasm; F = fibres; FS = fibre sclereids; IN = initial; L = lumen; LSW = lamellated secondary wall; N = nucleus; NT = non-tanniferous; P = phellem; PCS = pit canals in surface view; PF = Pholem fibres; PG = phellogen; PH = phloem; PR = phloem ray; PS = pholem sclereids; RS = ray sclereids; SC = secondary cortex; SPC = simple pit canals; SX = secondary xylem; T = tyloses; TA = thin areas in the wall; TN = tannin; TW = thin end wall; V = vacuole; VC = vascular cambium; WR = wood ray; YS = young sclereids.

Figs. 1–26. Fig. 1. Ground plan of a portion of a transection of a young root showing a strand of tanniferous cortical sclereids separated by parenchyma from the non-tanniniferous phloem sclereids and tanniniferous phloem ray sclereids. Note groups of fibres in the parenchymatous

cortex, × 8. Fig. 2. Ground plant of a portion of a transection of an old root showing a strand of tanniniferous cortical sclereids and phleom ray sclereids and non-tanniniferous phloem sclereids. All the three kinds of sclereids merge with each other (sclereids shown in black). Note the fibres in the cortical sclereid strand, phloem sclereids and in the phloem. Secondary xylem shows tyloses, × 8. Fig. 3. Portion of a transection of a root older than in Fig. 2. Tannin is not shown for the sake of clarity. Note that the broad sclereid zone includes fibres and fibre sclereids in the cortical strand of tanniniferous sclereids. Fibres can be seen among the non-tanniniferous phloem sclereids and phloem. All the cells of the phloem ray are tanniniferous and show sclereids in various stages of development in the distal region. It is difficult to delimit the sclereids in the cortical strand from those in the phloem rays and phloem. Tyloses are plenty in the secondary xylem vessels, × 47. Fig. 4. Portion of a tangential longisection through the cortical strand of sclereids (of a root of the same age as that in Fig. 3), showing cortical sclereids (tannin not shown), fibre sclereids and one fibre (to the extreme right), × 47. Figs. 5 to 26. Various kinds of sclereids from macerated roots. Tannin is not shown in any of them. Fig. 19. A group of different kinds of sclereids. Fig. 24. An extreme kind of osteosclereids. Figs, 25 and 26. two bizarre sclereids.

FIGS. 27–39. Figs. 27–33. Various elements ranging from a typical fibre (Fig. 27) to a fibre sclereid (Fig. 33). Fig. 30. A typical intermediate form a portion of which is enlarged in Fig. 31. Fig. 32. A portion of a typical fibre sclereid. Figs. 28 and 29 show variations in lamellatic ns in the wall and the frequency of pit canals in normal fibres. Fig. 30. × 65. Rest: × 287 Fig. 34. Portion of a transection through the secondaryc ortex of a root showing a sclereid initial and some young sclereids at various stages of development. Note the pit canals in one of them, × 287. Fig. 35. A group of a developing sclereids from a transection of an older root thrcugh the seondary cortex. Note tannin (cross hatched) in some and pit canals in a few others, × 287. Fig. 36. A group of developing sclereids in the secondary cortex from a tangential section of the root Arrow points to the apex of the root, × 287. Fig. 37. A developing fibre sclereid shcwn from a tangential section of the root through the secondary cortex. The fibre sclereid shows tannin and at one end the wall is thin. Arrow points to the apex of the root. This may even be a large osteosclereid in development, × 287. Fig. 38. A developing fibre sclereid in tangential section. Note its lamellated secondary wall, thin end wall, cytoplasm and the nucleus at this end and the cortical sclereid (tannin not shown). No pit canals have made their appearance. Arrow points to apex of the root, × 287. Flg. 39. A developing fibre sclereid in tangential section of a root. Note the pit canals in the lamellated secondary wall and cytoplasm and nucleus at the thin-walled end. The cortical sclereids (tannin not shown) show more pit canals than those in Fig. 38. Arrow points to the apex of the root, × 287.