GROWTH AND DEVELOPMENT OF SEPTATE AND CRYSTALLIFEROUS FIBRES IN SOME INDIAN TREES

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ABSTRACT

1. The development of septa in the wood fibres of two hardwoods, one ring-porous, *Lagerstroemia speciosa* (L.) Pers. and another diffuse-porous, *Protium serratum* (Wall. ex Colebr.) Engl. is reported.

2. Septa are formed in the fibres, as a result of the division of the protoplast which consists of true Karyokinesis followed by Cytokinesis at right angles to the long axis of the fibres, after the elongation of the cells is completed and secondary walls are laid in them.

3. The oldest fibre formed in a season, becomes septate first and the younger ones gradually become septate in centrifugal manner. The development of septa apparently takes place soon after the fibres attain maturity, as the fibres which fail to develop septa at the time remain non-septate.

4. Some correlation has been noticed between the time required for the fibres to attain maturity and the growth period. In *L. speciosa* in which the growth period is short, the septa are developed within a short time compared to *P. serratum*, which has a longer period of growth.

5. The number of septa formed in a fibre has been found to be more variable in *L. speciosa* than in *P. serratum*. The variability of this character and its reliability as a diagnostic feature in wood is discussed.

6. Crystalliferous fibres are formed in *L. speciosa* at the end of the growing season. Some of the septate fibres show nuclear division once again at that time. Each compartment divides into several locules and in each of them a crystal develops in the cytoplasm. The importance of crystalliferous fibres in the identification of woods is also discussed.

INTRODUCTION

Septate fibres are of common occurrence in the secondary xylem of many dicotyledonous families. They are seldom found throughout a family; even in a single genus all the species may not always show septate fibres (Metcalfe and Chalk, 1950; Spackman and Swamy 1949). Furthermore, the frequency and distribution of these fibres are known to vary from tree to tree and in some cases in different parts of the same tree (Chowdhury, 1954).

Standard text books on plant anatomy give rather scanty information on septate fibres and their importance in systematic classification of secondary xylem. Credit for throwing some light on this type of fibres goes to Vestal and Vestal (1940). They studied only one species, namely *Hypericum androesaemun* L. but by oversight did not give the ontogeny in detail. The present investigation was, therefore, taken up to find out its course of development from inception to maturity. In order to find out how the frequency of septate fibre varies in some species while in others it remains constant, two such types were selected for study, namely, *Lagerstroemia speciosa* (L.) Pers. and *Protium serratum* (Wall. ex Colebr.) Engl. These also represent the two main groups of dicotyledonous woods; the former belongs to the ring-porous group, while the latter to the diffuse-porous. Some preliminary notes have already been published on this investigation (Purkayastha 1953, Chowdhury *et al.* 1956). The present paper deals with the detailed information of the different stages of development of septate fibre up to its maturity. While studying *L. speciosa* (L.) Pers. it has been noticed that some septate fibres turn crystalliferous at the end of the growing season. Complete information on the formation of these crystalliferous fibres has also been included in the paper.

Material and Methods

Material examined consisted of both elongating current year's shoots and mature one to two year old branches. For each species five trees growing in New Forest, Dehra Dun, were selected, and their growth data recorded. The material was collected at weekly intervals till the fibres became septate and later on at fortnightly intervals till the cessation of growth in November. The older shoots were collected only after the commencement of radial growth. All material was fixed in Formalin-Acetic-Alcohol at a time when the nuclear division associated with the formation of septa was most active. The best time for the taking out material, which was determined after several trials, was found to be different for the two species. In *L. speciosa* the best time was found to be between 6.30 and 7.30 a.m. while in *P. serratum* between 5 p.m. and 6 p.m.

The study was mainly based on a large number of longitudinal sections cut on a sliding microtome and stained in Heidenhein's Haematoxylin and saffranin. The results obtained during the first year of study were confirmed by observations made during the second year. There was little difference between the materials collected in two years.

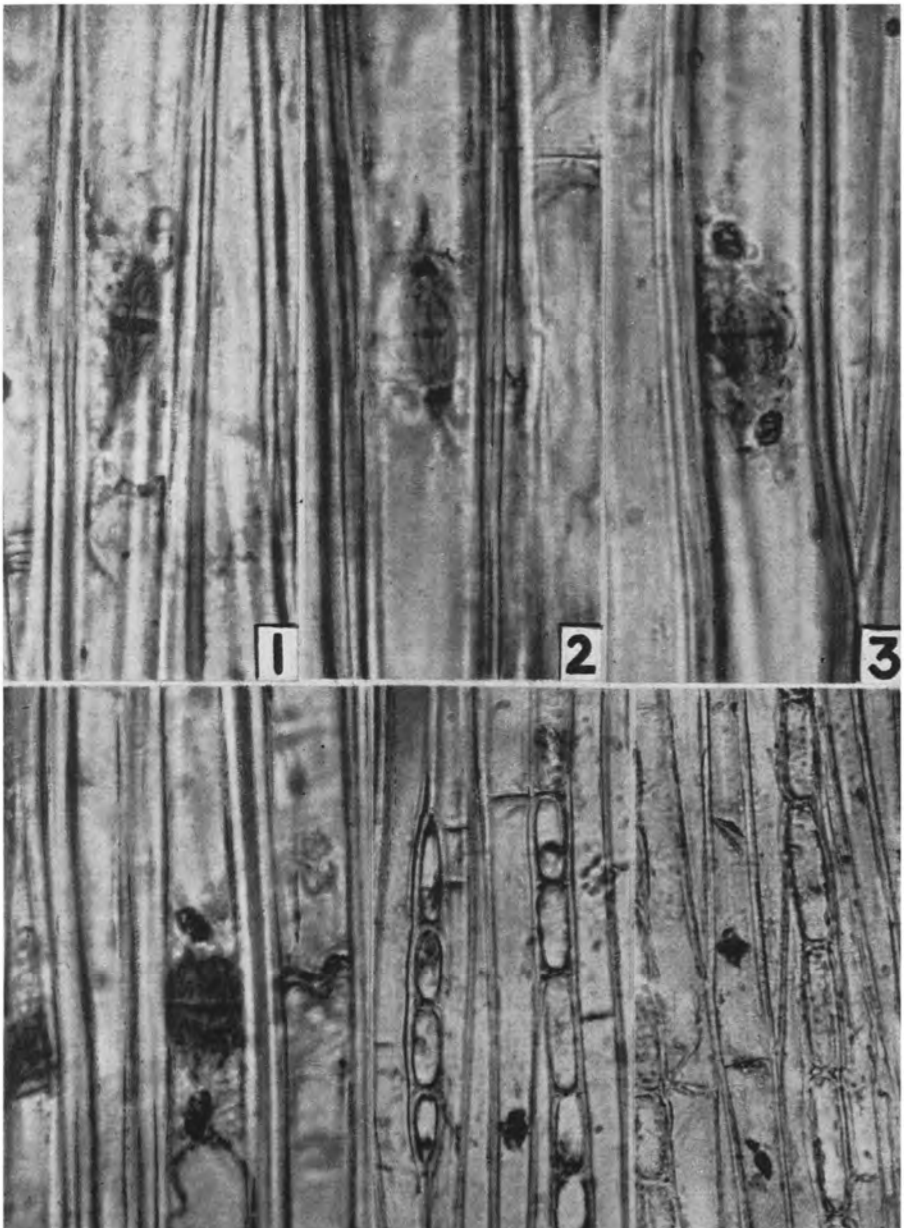
Results

I. *Lagerstroemia speciosa* (L.) Pers.

The trees at Dehra Dun are generally leafless during February and March. In the latter part of March, new buds start coming out from the axils of the leaves, as indicated by scars. These start growing into new shoots by the end of March. The extension growth of these shoots is generally completed in ten to fifteen days. The flowering shoots also come out about the same time. A second flush of extension growth takes place usually in the beginning of July and continues also for about a fortnight. The second extension growth is rather irregular in this species, some branches not having it at all. In most of the branches after completion of the first height growth, the terminal buds drop off. In many of them, however, new buds developing from the axils of the terminal leaves take the place of terminal buds and start growing again in July. At the same time, new buds can also be seen developing on the older branches, which have not grown during the first height growth. This type of irregular growth of shoots from older branches has been observed from the beginning of July till October. Occasional development of flowering shoots has been noticed even in December. Leaves are shed in January or early February. The radial growth in the older branches has been observed to take place long after the completion of the first extension growth. The cambium in these branches remains inactive till late July or the early part of August.

Formation of septate fibres in the elongating shoots.

The septa are formed about two weeks after the fibres are cut off from the cambium. By this time the elongation is completed and the secondary walls of the fibres are fully laid down. The first fibres to become septate are those in the region nearest to the protoxylem vessels at the base of the shoots. From here the formation of septa gradually spreads outwards towards the cambium and also upwards towards the tip of the shoot.



Figs. 1–3, *Lagerstroemia speciosa* (L.) Pers. Stages in the formation of septa; 1, Metaphase 2, early telophase; 3, late telophase. Fig. 4, *Protium serratum* (Wall. ex Colebr.) Engl. radial section showing progressive development of septa from inside (right) to outside (left) (× 1500). Figs. 5 and 6, stages in the development of crystalliferous fibres; 5, division of the nucleus in one of the compartments of a septate fibre; 6, simultaneous division of nuclei of different compartments of a septate fibre (× 450).

The formation of septa in the fibres is by nuclear division followed by cytokinesis at right angles to fibre walls. All fibres before the formation of septa, are characterised by an oval elongated nucleus, with a single nucleolus. The nucleus passes through the usual changes during division. The spindle figure becomes apparent at the close of the *prophase*. In *metaphase*, the spindle is generally seen at an angle to the long axis of the fibre (Fig. 1). In *telophase*, the phragmoplast begins to extend laterally in the equatorial region till it touches the walls of the fibre (Figs. 2 and 3). The cell plate is formed in the equatorial region which divides the fibre lumen. The daughter nuclei pass into the resting stage after migrating to the centre of the newly formed compartments. The septumfinally develops in the region of the cell plate and in staining behaviour resembles middle lamella. In the mature wood the septa appear to be composed mostly of lignin. They are completely dissolved by repeated chlorination and subsequent treatment with dilute ammonia but they are insoluble in 72 per cent sulphuric acid.

Although formation of septa is evidently correlated with cell maturation, it has been noticed that in the newly formed shoots, nuclei of a few fibres fail to divide on attaining maturity, and as a result, these fibres remain non-septate. Apparently these nuclei do not divide later.

Formation of septate fibres in the older branches.

The septate fibres are formed in a similar manner about a fortnight after they are cut off from the cambium. The newly formed fibres adjacent to previous year's wood become septate first and gradually the fibres nearer cambium become septate. The septate fibres in the elongating shoots, however, differ from those in the older branches as regards the number of septa they contain. In the elongating shoots the septate fibres are generally partitioned by a single septum, whereas those in the older stems are usually divided by three septa, although fibres with one or rarely two septa, are sometimes met with. These septa are formed by a second division of the daughter nuclei after the formation of the first septum. The occasional presence of fibres having one or two septa is due to the failure of both or one of the daughter nuclei to divide again.

Formation of crystalliferous fibres.

After the formation of septa, the nuclei in the fibres remain in 'resting stage' for a long time. The nuclei are visible in these fibres till heavy deposition of starch occurs in them. The starch deposition takes place twice in a year, once in June in the shoots developed in April and again in November in the later formed tissues. Along with the deposition of starch some of the septate fibres, particularly those contiguous to longitudinal parenchyma and rays, also become crystalliferous. These fibres are then subdivided into small locules in which solitary crystals develop.

The first stage in the formation of crystalliferous fibres is the renewed mitotic divisions in the septate fibres. The fibres, which ultimately become crystalliferous, are distinguished from the others by their enlarged nuclei and deeply stained protoplasts. The stages in the division are similar to those already described except that the daughter nuclei divide several times, successively and simultaneously, and the fibre is subdivided into small locules within a short time (Figs. 5 and 6).

Each of the locules thus formed, contains a round nucleus in the centre surrounded by a thick mass of cytoplasm without any vacuoles. The crystal first appears as a small cytoplasmic inclusion, which is an exact replica of the fully grown crystal in shape. As the crystal grows, it pushes the cytoplasm and the nucleus to the periphery and ultimately the cytoplasm forms just a lining round the crystal. The nucleus, however, remains prominent throughout the development of the crystal.

Generally all nuclei in a fibre divide and the entire fibre becomes crystalliferous. But nuclei of all the compartments of a septate fibre always may not take part in the formation of these locules which ultimately become crystalliferous. Occasionally only half of them divide to form the crystalliferous locules while the other half remains unchanged.

II. *Protium serratum* (Wall. ex Colebr.) Engl.

In this evergreen species also two distinct periods of extension growth have been observed. However, the extension growth in this species differs from that of *L. speciosa* in some respects. All the barnches in *P. serratum* grow during both the periods of extension growth and the terminal buds do not fall off after the height growths are over. The first extension growth starts in the beginning of March and continues for about 3–4 weeks. By the middle of April generally all the leaves of the new shoots are fully mature. It is about this time, that the previous year's leaves turn yellow and start falling off. The second extension growth generally starts by the middle of June and also continues for about a month.

As in *L. speciosa* no activity of the cambium of the older branches has been noticed during the first extension growth. The diameter growth in these parts usually starts by the end of June or the first week of July.

The development of septa in the fibres takes place first in the oldest fibre formed in a season and then gradually in the younger ones, as in *L. speciosa.* In the elongating shoots, the formation of septa is noticed first in the fibres nearest to the protoxylem vessels, when the shoots are about four weeks old. In the older branches also the septa are developed in the fibres, adjacent to the previous year's wood, about a month after the initiation of radial growth. The stages in the formation of septa are similar to those of *L. speciosa* (Fig. 4). However, both in elongating shoots, as well as in older branches, the nuclei of the fibres, after attaining maturity, divide several times and consequently a varying number of septa are formed in the fibres. Moreover, as the fibres mature, the nuclei of all the fibres divide with the result no fibres remain non-septate. The septa, although similar to *L. speciosa*, are more resistant to the chemical action.

As in *L. speciosa*, the nuclei in the fibres are visible throughout the year till the visibility is obscured by heavy deposition of starch, which appear to be correlated with the slackening of growth. Unlike *L. speciosa*, however, the nuclei in these fibres do not show any division again at this time and no crystalliferous fibres are formed.

Discussion

Considerable work has been done by Chowdhury and Tandan (1950) on the growth of broad-leaved trees of India. They have found that extension growth usually precedes radial growth by about 2 weeks to 3 months, in both ring-porous and diffuse-porous species. Their observations differ considerably from those reported from Europe and North America where both the height and the diameter growth start simultaneously. The difference observed between the time of initiation of extension and radial growth in both these species confirms Chowdhury and Tandan's findings.

The stages in the division of the protoplast associated with the formation of septa are similar to those described by Vestal and Vestal. However, in the two species investigated, there are some differences as regards the time required for the development of septa and in the number of septa formed in a fibre. These are tabulated below :—

Species	Time required for the development of septa in the fibres	Number of septa formed per fibre		Nature of deposits in the fibres
		In elongating shoots	In older branches	
L. speciosa	about 2 weeks	1, a few also remaining non-septate.	3, but occasionally less.	Starch but a few fibres also become crystalliferous.
P. serratum	about 4 weeks	3 or more.	3 or more.	Starch, but no crystals.

Since septa are developed after secondary walls are laid down, their formation may be taken as an indication of the maturity of the fibres. The development of septa in the fibres from the oldest to the youngest in a centrifugal manner also suggests that the formation of septum takes place immediately after the fibres attain maturity. It is interesting to note in this connection the apparent correlation between the growth period and maturity of the fibres. In the ring-porous *L. speciosa*, the septa are developed when the fibres are about two weeks old and the extension growth is also completed within this period. Whereas in the diffuse-porous *P. serratum* the septa are developed after about 4 weeks and the extension growth also continues for about a month. The occurrence of fewer number of septa and the occasional presence of non-septate fibres in the elongating shoots of *L. speciosa*, probably indicates the comparatively variable nature of this character in this species. A preliminary survey of the septate fibres in the wood of some families like *Anacardiaceae*, *Burseraceae*, *Combretaceae*, *Euphorbiaceae*, *Meliaceae* and *Lauraceae* has also shown that although the presence of septate fibres is generally a constant feature for a species, in some of the woods the percentage of septate fibres and the number of septa per fibre may vary in a similar manner. More observations on this point are necessary to bring out the true significance of this character as a diagnostic feature.

The nuclear divisions which precede the formation of crystalliferous locules are similar to those of the formation of septa in the fibres. However, the nuclei of different compartments of a fibre, divide several times and these divisions take place simultaneously. Similar simultaneous division of the nuclei in the phloem fibres of tobacco has been reported by Esau (1938). In these phloem fibres, however, the karyokinesis is not followed by cytokinesis which results in multinucleate condition. In the formation of crystalliferous locules, on the other hand, normal division of the protoplast occurs and septa are formed in the region of the cell plate during cytokinesis.

It is generally believed that Calcium oxalate is an excreted waste product of plant metabolism. Milanez, quoted by Chattaway (1937), has suggested that the frequent occurrence of crystals in the terminal parenchyma (as in many of the Caesalpinaceae) may be the result of the accumulating of waste products from the activity of the entire growing season. The development of crystals, both in the wood fibres as well as in other woody tissues, at the end of the growing season lends support to the view expressed by Milanez. Chattaway, however, thinks that although this is a very probable explanation of the crystals in the chambered parenchyma, it does not seem equally applicable to the solitary crystals that are often found scattered irregularly in rays and parenchyma.

A survey of the literature reveals that crystalliferous fibres have been grouped under two classes by some workers (Metcalfe and Chalk, 1950 ; Pearson and Brown 1932). Some septate fibres show only a few septa and only some of these chambers formed thereby contain crystals. On the other hand, some such fibres are subdivided into small locules and in each of these locules or chamber crystals are formed as in *L. speciosa*. The value of the latter type of fibres for generic classification of wood appears to be good, but needs further confirmation.

In this connection, the difficulty of detection of crystalliferous parenchyma and crystalliferous fibres must be pointed out here. Chattaway (1937) while working on *Sterculiaceae* reported presence of crystalliferous fibres in *Sterculia*. Milanez (1937, 1939), however, questioned it because he was of the opinion that these crystal cells in *Sterculia* are parenchymatous in origin and not prosenchymatous. This was later confirmed by Chattaway (1939) herself. All these mean that one has to be very careful in describing the presence of crystalliferous fibres and crystalliferous parenchyma. A mere examination of sections depicting different views of a block of wood may lead to confusion. The final classification of these crystalliferous elements will rest on the examination of the macerated material.

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