Developmental changes in the vascular cambium of *Delonix regia* Rafin

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Abstract. The developmental changes occurring in the vascular cambium of *Delonix regia* have been studied in different age group trees having different circumferential central axis. It has been found that the cambial cells undergo considerable variation both in their number and dimension with the growing age. The fusiform initials experience a linear expansion by local apical growth, while the ray initials undergo rapid multiplication. The former loses ability of apical expansion and the latter continues to multiply and occupy more area of the cambial cylinder with increasing age.

Keywords. Cambium; fusiform initials; ray initials; apical growth; pseudo-transverse division; *Delonix regia*.

1. Introduction

*Delonix regia* Rafin is a medium to large size deciduous leguminous tree commonly cultivated in the gardens throughout the tropical and subtropical plains of the Indian subcontinent. It grows fairly well at Aligarh which is located in the monsoon belt of the Great Gangetic plain at 27° 53’ N latitude and 78° 4’ E longitude. The present authors had earlier given a preliminary account of cambial structure of this species (Ghouse and Hashmi 1977). The present paper deals with the developmental changes in the cambium as the tree ages.

2. Materials and methods

Cambial samples of 2 cm² together with some sapwood and bark were obtained from the main trunk of *Delonix regia*, growing in the university gardens in Aligarh. Similar samples were collected from five different age group trees whose trunks ranged from 30 to 300 cm in circumference. Five trees were sampled in each age group and from each tree four samples were collected, one each from the east, west, north and south side of the tree. All samples were collected in the morning hours between 6:00 to 8:00 a.m. with the help of a chisel and hammer from the main trunk of the trees, at chest height. The samples were fixed on the spot in...
FAA and aspirated after an hour. They were transferred to 70% ethanol after a week for preservation. Sectioning was done on a sliding microtome at a thickness of 10 to 12 μm in transverse, tangential and radial longitudinal planes. The sections were stained in tannic acid and iron chloride (Foster 1934) or with iron alum hematoxylin combination, dehydrated in ethanol and xylol series and mounted in Canada balsam.

From each sample, 100 elements of each category were measured on a random basis. The average and range of size given in this report are based on measurements taken out of all samples obtained for each age group tree. Similarly, all data given in this report regarding the dimension of fusiform and ray initials and their relative proportion and also about the cambial rays based on all samples pertaining to a particular age group. In all cases, the individual variation from tree to tree of the same age group has been ignored.

In the present report, the word cambium has been used in a broad sense to include the whole population of undifferentiated cells situated between the xylem and phloem.

To calculate the ratio of ray and fusiform initials, the area occupied by the respective initials in the tangential sections was taken as the basis. For this purpose 25 camera lucida drawings were made on rice papers out of every sample and the relative proportion was calculated on the basis of their weights following the method described by Ghouse and Iqbal (1975).

3. Observations

The vascular cambium of *D. regia* forms a continuous ring. It is non-stratified and consists of the fusiform and ray initials (figure 1C). The former has long lateral walls and pointed end-walls and the latter is roughly isodiametric. The fusiform initials undergo considerable size variation, as the tree ages. They gradually increase in their length average with the increasing circumference of the tree axis, but later tend to stabilize in length (table 1). The ray initials, however do not undergo any dimensional change. But the number of ray initials per unit area and in a ray increases considerably as the tree ages.

In tangential view, the ray initials are homogeneous. The rays are mostly fine and they vary from 1–3 cells in width and 1–25 cells in height. The number of comparatively tall rays per unit area gradually rises with the increasing age (figure 2). Similarly, more multiseriate rays are found in older trunks than in the younger ones (figure 3). In general, the cambial rays are short and fine in *D. regia* but at times one or more contiguous rays fuse together to form tall ray bodies (figure 1C). Contrary to the above, the intrusion of certain fusiform cells into a panel of ray initials also sometimes occurs, resulting in the splitting of tall ray bodies into two or three small entities (figure 1F).

The growing number of ray initials in the older trunks causes a considerable change in the relative proportion of ray and fusiform initials in the cambial zone. Depending on the age of the trunk, the area occupied by the ray initials varies from 16 to 21% the minimum in the youngest and the maximum in the oldest trunk analysed (figure 4).
Figure 1. Photomicrographs of cambial samples of *Delonix regia*, as seen in tangential view. A, B show the formation of new ray initials from a laterally cut initial cell (arrows); C, the nonstratified arrangement of initials and the fusion of cambial rays; D, a short fusiform initial; E, a newly formed anticlinal wall; F, splitting of a ray. A, B, D, E and F are at × 248; C at × 98.
Table 1. Size variation of cambial initials in tree axes of *Delonix regia* having different circumference. The figures given in the parentheses indicate the range.

<table>
<thead>
<tr>
<th>Circumference in cm</th>
<th>Size of fusiform initials (μm)</th>
<th>Size of ray initials (μm)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Width</td>
</tr>
<tr>
<td>30</td>
<td>322</td>
<td>20</td>
</tr>
<tr>
<td>75</td>
<td>365</td>
<td>20</td>
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<tr>
<td>150</td>
<td>430</td>
<td>22</td>
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<tr>
<td>225</td>
<td>466</td>
<td>24</td>
</tr>
<tr>
<td>300</td>
<td>462</td>
<td>24</td>
</tr>
</tbody>
</table>

Figure 2. Histograms show the frequency of short, medium and tall ray types in the cambial zone of tree axes having different circumference. *C*₁, 30 cm; *C*₂, 75 cm; *C*₃, 150 cm; *C*₄, 225 cm; *C*₅, 300 cm.

The fusiform cambial initials undergo pseudotransverse anticlinal divisions (figure 1E) to multiply in number to cope with the expanding size of the trunk due to secondary growth. These divisions give rise to two daughter cells of equal or unequal size. Such newly formed anticlinal oblique walls measure from 25 to 85 μm with an average of about 55 μm. Similar measurements of oblique end walls of mother cells show that they vary from 25 to 130 μm with an average of 71·6 μm (table 1). It appears that the end walls of the daughter cells elongate a little during their development. This apical elongation shows a progressive increase with the increasing age till the trunk attains a circumference of 225 cm and later they appear to lose their ability of apical elongation with the further increase in size of the trunk.
The short fusiform initials (figure 1D) which usually form from the unequal anticlinal division of the mother initials generally give rise to ray initials by undergoing repeated transverse divisions. In addition, there appears to be additional means of new ray initial producing mechanism in *D. regia*. Sometimes new ray initials form as apically isolated segments of a normal fusiform initial and many a time ray initials are produced as lateral lens-shaped cells (figure 1A, B).

4. Discussion

In *D. regia* as in the majority of dicotyledons and gymnosperms, the vascular cambium forms a complete ring in the shoot axis. Although a number of leguminous plants have been shown to possess a cambium of stratified type (Bailey
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1923; Ghouse and Yunus 1974a, b; Ghouse et al 1973), D. regia has a non-
stratified cambium.

It is well known that the average size of cambial initials varies with the age of
the cambium. The studies of Bailey (1923), Bosshard (1951), Hejnowicz and Hejno-
wicz (1958), Bannan (1962), Callquist (1962), Evert (1963), Ghouse and Yunus
(1973) and Ghouse and Hashmi (1980) clearly indicate that the length average of
fusiform initials increases with the increasing age of cambium till the cells reach
their maximum limit and later more or less stabilize in length. The data recorded
in the present study on the length average of fusiform initials in various age group
trees with progressively widening trunks also reveal the same for D. regia.

Bailey (1923) has noted anticlinal divisions in fusiform cambial initials to be
of two types viz. radial longitudinal and radial oblique or pseudotransverse, the
latter being the characteristic way of cell division of cambial initials in the non-
stratified cambia. In D. regia, the cambium being a nonstratified type, the cambia-
initials undergo radial oblique divisions to produce daughter cells of equal or un-
equal size, depending on the position of the cell plate formation. The anticlinal
divisions have been reported to be generally restricted to the cambial initials in
conifers and dicotyledons (Cumbie 1967) but in the present study such divisions have
been noted throughout the cambial zone, as has been reported in certain rare cases
like Hibiscus laciocarpus (Cumbie 1963) and Acer pseudoplatanus (Catesson 1964).
The age of the tree, its vigour, the amount of pressure created by secondary xylem
and the fruiting habit of the plant have been reported to regulate the occurrence
of anticlinal divisions in the fusiform cambial initials by different workers (Bannan
1960; Evert 1961; Srivastava 1963; Wilson 1966; Cumbie 1967). In the present
study, higher rate of anticlinal divisions has been noted in the younger age group
trees rather than in the older ones as has been noted by Wilson (1966) in Pinus
strobus and in Prosopis spicigera by Ghouse and Iqbal (1977).

The daughter cells resulting from a radial oblique division usually undergo apical
elongation in D. regia as reported by Bannan and Whalley (1950), Bannan (1956,
1960) and Hejnowicz (1961). In the present study the ability to undergo apical
elongation has been observed to depend on the age of the cambium (Ghouse
and Hashmi 1980). Since the apical elongation adds to the total length of the
elements, the latter also depends on the age of the cambium. The length of the
sloping end walls and the total length of the elements run therefore parallel to
each other with respect to the age of the cambium.

The ray initials form an integral part of the cambium and contributed a consi-
derable proportion of the cambial cylinder. Barghoorn (1940a, b), Braun (1955),
and Yunus (1973), Ghouse and Iqbal (1977) and Ghouse and Hashmi (1980)
have worked out the origin and development of ray initials in some dicotyledons.
The recorded observation regarding the ray initial development in D. regia in
the present study indicates that the ray initials originate in more ways than one.
They not only arise out of the short fusiform initials but also from cells either
cut apically or laterally, as has been reported in the case of Dalbergia sissoo
(Ghouse and Yunus 1973) and Polyalthia longifolia (Ghouse and Hashmi 1980).
The increase in the number of ray initials in older trunks, observed in the present
study, accords with the earlier reports from our laboratory on Dalbergia sissoo
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(Ghouse and Yunus 1973), *Prosopis spicigera* (Ghouse and Iqbal 1977) and *Polyalthia longifolia* (Ghouse and Hashmi 1980). The increasing population of cambial rays is generally brought about by the formation of new panels of ray initials out of the fusiform initials. This, as a consequential measure, in turn brings about the formation of complex ray bodies, particularly when the fusiform initials situated between the rays get converted into a number of ray initials. Formation of such composite rays has been noted by several earlier workers like Barghoorn (1941), Evert (1961, 1963), Ghouse and Yunus (1973, 1974a), Ghouse and Iqbal (1977) and Ghouse and Hashmi (1980). In contrast, the splitting of tall and exceptionally broad rays by the intruding action of fusiform initials has been observed in the species presently investigated. Splitting of rays into a number of small entities, as it occurs in *D. regia*, has also been noticed in several other hard wood species by a number of earlier workers (Chattaway 1933, 1940a, b; Evert 1961; Cheadle and Esau 1964; Ghouse and Yunus 1973, 1974a, b; Ghouse and Iqbal 1975, 1977; Ghouse and Hashmi 1980).

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