ANATOMY OF BRANCH ABSCISSION IN *LAGERSTROEMIA MICROCARPA* WIGHT

BY K. V. BHAT*, T. SURENDRAN† AND K. SWARUPANANDAN‡

*Division of *Wood Science, †Physiology and ‡Ecology, Kerala Forest Research Institute, Peechi 680 653, Kerala State, India*

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SUMMARY

Some anatomical details of branch abscission in *Lagerstroemia microcarpa* Wight (Lythraceae) are discussed. Repeated abscission of numerous annual twigs and subsequent healing of their scars produce irregular growth of the subjacent branch portions to give gall-like structures. In the abscission zone, secondary xylem fibres are thin walled and poorly lignified, with dense protoplasmic contents and closely spaced septa. Disintegration of pith parenchyma cells and shrinkage of bark and wood tissues contribute towards weakening of abscission zone. The protective zone situated proximal to the abscission zone is strongly lignified and rich in extractives. Detachment occurs immediately above the protective zone leaving the encircling dormant buds intact. Abscission scars are healed centripetally by the usual method of callus formation from the cambial tissue. It appears that branch abscission in *L. microcarpa* is a mechanism to withstand drought by reducing the transpiring surface.

Key words: Branch abscission, abscission zone, septate fibres, wound healing, *Lagerstroemia microcarpa*.

INTRODUCTION

Abscission, the phenomenon of shedding plant parts is of wide occurrence in nature. Leaves, shoots, flowers, fruits and seeds are some of the structures that commonly abscise. This rejection mechanism operating in plants (Kozlowski, 1973) involves complex physiological changes influenced by both internal and external factors (Addicott, 1978). The manifestation of these changes is the formation of an 'abscission zone' and subsequent detachment of the organ at this site. Plant parts, however, may also be lost by mechanical damage or by death and withering. In such cases no abscission zone is formed.

Abscission of branches, also known as 'cladoptosis' (Büsgen & Münch, 1929; Millington & Chaney, 1973) is not so well known as that of leaves, flowers and fruits in spite of the fact that a number of woody perennials regularly shed their shoots, branches or twigs (Pijl, 1952, 1953). This subject has received rather limited research attention, 'the paucity of studies on this phenomenon [being] astounding in view of its influence on the form of woody plants and on the value of lumber obtained' (Millington & Chaney, 1973). Abscised branches form a substantial portion of the forest litter (Kozlowski, 1973) and it is believed that branch abscission enables the plants to withstand drought. Apart from its ecological and silvicultural implications this behaviour is of considerable academic interest, especially its impact on plant growth and development.

Tropical deciduous trees often shed their shoot tips, branchlets or twigs following seasonal leaf fall in summer. This process is of significance in determining the branching pattern and architecture, and also in development of particular

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morphological characteristics (Addicott, 1982). In *Lagerstroemia microcarpa* Wight (Lythraceae) a tropical deciduous tree common in moist deciduous forests of Western Ghats (India), repeated annual shedding of the terminal branchlets leads to enlargement of the subjacent portions of branches into irregular gall-like structures. This paper presents some anatomical observations on branch abscission in this species and attempts to trace the formation of such tubercular structures.

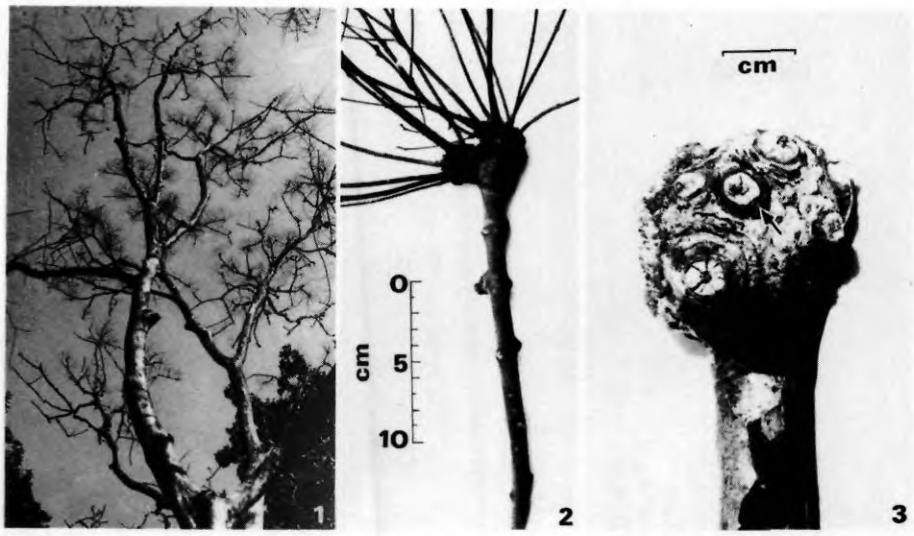
MATERIALS AND METHODS

Branch material for the present study was collected from mature trees of *L. microcarpa* (Fig. 1) growing naturally on the campus of Kerala Forest Research Institute, Peechi. Branches having distinct gall-like structures with intact branchlets (Fig. 2) were fixed in FAA (Johansen, 1940). Material was collected during a growth season, in June, soon after flushing, in December, when leaf shedding was in progress and branchlets started drying up, and in the following March, after completion of leaf fall and drying of branches. For anatomical observations 15 μm thick sections were cut on a Reichert sliding microtome. Sections were stained with safranin–fast green (Johansen, 1940) and with toluidine blue O (O'Brien, Feder & McCully, 1964). Phloroglucinol-HCl (Johansen, 1940) was used to examine lignification.

RESULTS AND DISCUSSION

Branch abscission in *L. microcarpa* is preceded by seasonal leaf shedding which begins in the latter part of the growing season. The terminal branchlets borne on gall-like tubercles slowly start drying up as the leaf fall continues. By the time that shedding of leaves is complete, bark of the naked twigs appears totally dry with transverse cracks. The tubercles bearing numerous dry twigs are distinctly visible at this stage (Figs. 1 and 2). It is likely that desiccation of twigs probably leads to their partial separation. However the detachment of twigs is largely mechanical and is facilitated by wind. As in the tumbleweed, *Kochia scoparia* Schrad. (Becker, 1978), brittleness of the abscission zone upon drying appears to be the main reason for the rupture rather than weakening of the tissue by a physiological mechanism. Similar mechanical separation has also been reported in the leaf abscission zones of guayule (Addicott, 1945). Abscised twigs range from 20 to 40 cm in length and 2 to 5 mm in diameter. The tubercles devoid of twigs show numerous circular branch scars (Fig. 3) which are slightly concave but rough due to the absence of a protective layer. Stereoscopic examination reveals the presence of three or more dormant buds encircling each scar (Fig. 3, at arrow).

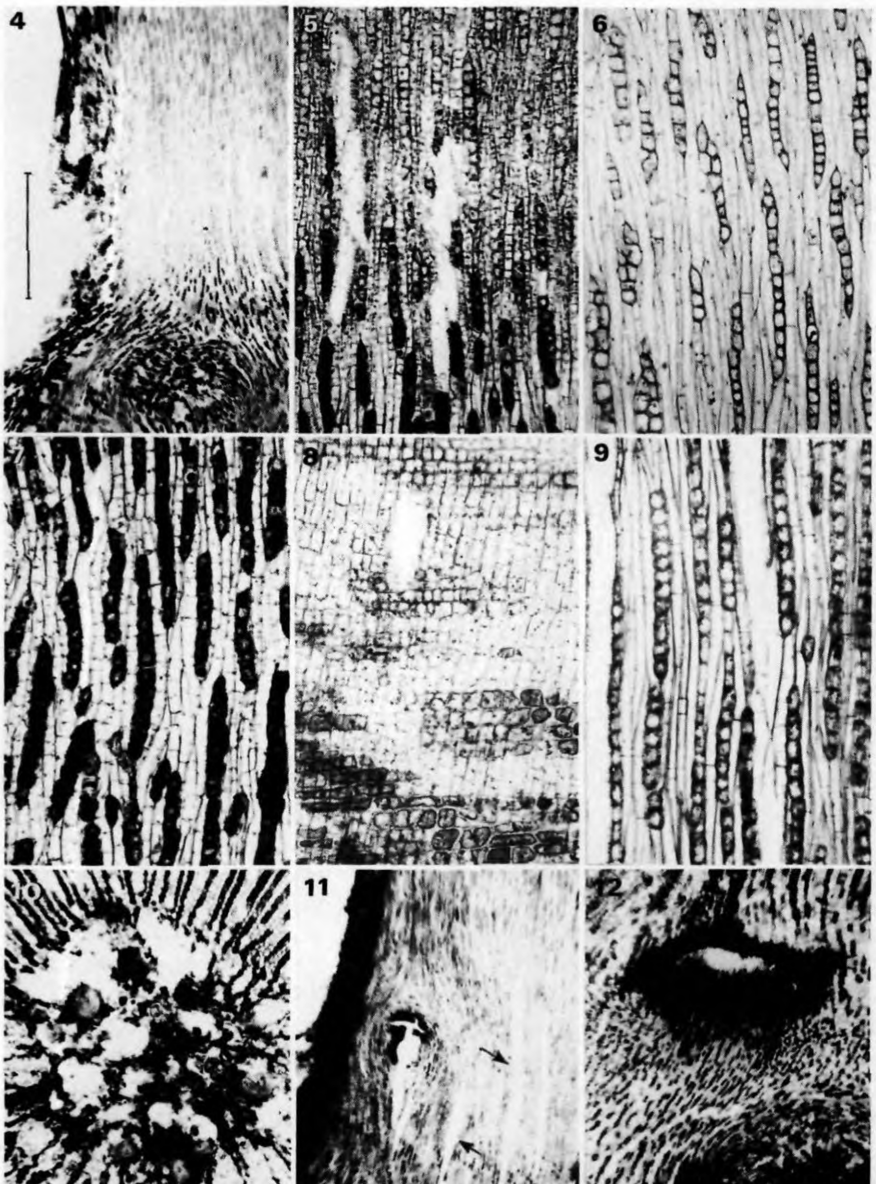
After the onset of the monsoon in June the tubercles resume growth by producing a large number of new shoots from the dormant buds. Among the young shoots a few grow more vigorously than the rest. It appears that these two types of shoots differ physiologically from each other; the vigorous shoots are retained by the tree while all the weaker ones are abscised, in late summer. In those shoots which persist, abortion of shoot tips follows leaf shedding and arrests the terminal growth. Branch vigour is considered to be an important factor influencing cladoptosis (Chaney & Leopold, 1972; Millington & Chaney, 1973; Eames & MacDaniels, 1947) and in white oak, where ethephon application enhanced cladoptosis, the branches which abscised were found to be the less vigorous ones with smaller terminal shoots (Chaney & Leopold, 1972).



Figs. 1 to 3 Fig. 1. A mature tree of *Lagerstroemia microcarpa* after leaf shedding in summer; note the gall-like enlargements bearing twigs. Fig. 2. A single such branch showing a tubercular structure with many dry twigs. Fig. 3. A tubercle with distinct abscission scars after the twigs are shed; arrow shows a dormant bud.

Structural changes leading to the establishment of branch abscission zone take place in *L. microcarpa* when leaf fall is in progress. The basalmost 1 to 1·5 mm portion of the branchlets with characteristic histochemical and histological features constitutes the abscission zone. Fibres and vessels of secondary xylem show feeble cell wall staining in this zone (Figs. 4 and 5). Use of the phloroglucinol-HCl test confirmed that these elements are poorly lignified in contrast to the region further below (see Fig. 4). Towards its distal limit the abscission zone gradually merges with moderately lignified secondary xylem from which it is not clearly demarcated. Similar observations have been made in *Perebea mollis* (Poepp. & Endl.) Huber and *Naucleopsis guianensis* (Mildbr). C. C. Berg with regard to the transition between abscission tissue and normal xylem (Koek-Noorman & ter Welle, 1976). Samples collected in June showed that in the region of the future abscission zone, xylem elements are apparently thin walled and less lignified (Fig. 6). However, the difference in lignin content appears strikingly prominent at later stages, probably due to continued lignification in other parts especially those proximal to the abscission zone. Once the twigs are shed the exposed proximal region with its thick walled, strongly lignified fibres, probably acts as a protective zone. It is supported by the fact that all the rays at this level of the branchlet, and sligthly above, where the mechanical rupture occurs show dense accumulation of dark brown contents (Figs. 5 and 7) – a feature not found elsewhere in young branchlets. Substances such as polyphenols, tannins and resins, often found deposited within xylem tissue, are generally believed to serve a protective function owing to their toxic or repellent properties. Species that do not produce such substances are prone to severe damage by microorganisms (Addicott, 1982).

Anatomical studies on branch abscission are rather limited; however, poor lignification of the abscission zone (Eames & MacDaniels, 1947; Koek-Noorman & ter Welle, 1976; Osborne, 1984) and presence of a well defined protective layer



Figs. 4 to 12. Fig. 4. Tangential section at the base of a branchlet showing feeble staining of abscission zone and densely stained protective zone below. Fig. 5. Enlarged view of the same region; note the deposition of extractives in ray cells of the protective zone. Fig. 6. Secondary xylem atthe branchlet base showing thin walled, poorly lignified fibres in the future abscission zone. Fig. 7. Dense accumulation of extractives in ray cells; note the septation of fibres. Fig. 8. Radial section of the abscission zone to show septation of fibres. Fig. 9. Portion distal to the abscission zone with normal, thick walled, lignified fibres. Fig. 10. Cross-section of a twig at the abscission zone to show partly disorganized pith tissue and cavities produced thereby. Fig. 11. Longitudinal cracks (arrows) in the abscission zone due to shrinkage of the tissue. Fig. 12. An abscission scar overgrown by irregularly oriented wood tissue. Inserted scale represents 650 μm for Figs. 4, 11 and 12; 285 μm for Fig. 10; 210 μm for Fig. 5; 155 μm for Fig. 6; 140 μm for Figs. 7 and 9, and 130 μm for Fig. 8.

or periderm have been observed in some species (Eames & MacDaniels, 1947; Licitis-Lindbergs, 1956), and lignification of protective tissues after the branch fall has also been recorded (see Millington & Chaney, 1973). Similarly, in the leaf abscission zone, lignin is found to be characteristically low or absent, the protective layer becoming conspicuously lignified prior to, or after the leaf fall (see Webster, 1973).

Thin walled fibres of fully developed abscission zone are found transversely subdivided by septa into squarish segments each with a single prominent nucleus and dense cytoplasm (Figs. 7 and 8). Normal septate fibres found in distal region possess thicker walls and widely spaced septa (Fig. 9). Koek-Noorman & ter Welle (1976) also observed larger nuclei in fibres of the abscission zone but found no appreciable difference in the wall thickness as compared to the normal wood. A small proportion of fibres are highly segmented even in the normal wood of *L. microcarpa*. Such fibres usually lie contiguous to rays and contain crystals (Pearson & Brown, 1932), but the nuclei are less prominent in them. Nuclear divisions and subsequent septation seem to take place late in the growing season. Samples collected in June showed only few septa in fibres at the branch base (Fig. 6). Septation of fibres is often very conspicuous towards the lower end of the abscission zone which is the future region of detachment. It appears therefore, that active divisions within the fibres may weaken the xylem tissue and thus facilitate its rupture.

Tissue weakening at the abscission zone is further aided by changes in the organisation of pith, while desiccation of tissues equips the twigs for the rupture. However, occlusion of vessels by tyloses or other deposits was not found in the abscission zone. The pith tissue composed of parenchyma cells, sclereids and sac-like idioblasts is slightly dilated at the branch base, as in *Agathis* (Licitis-Lindbergs, 1956), but no appreciable reduction in the amount of xylem is found. With the completion of septation in fibres many of the parenchyma cells become disorganized leaving irregular cavities within the pith (Fig. 10). The disintegration is confined to the swollen basal portion of the pith which lies at the same level as the abscission zone. No further cellular changes are evident in the abscission zone. Nevertheless, shrinkage due to desiccation produces transverse cracks in the bark which may sometimes extend inwards into the weaker xylem portion. Often the xylem tissue splits longitudinally along the vessels and rays suggesting excessive shrinkage of the abscission zone (Fig. 11, at arrows). The twigs at this stage are readily detachable with the aid of wind. The level of detachment lies slightly distal to the position of dormant buds and hence, the latter remain undamaged when twigs are shed and the scars left open.

The exposed transverse surface of the xylem is soon overgrown by callus tissue. The growth of callus is centripetal from the cambial zone as judged by the orientation of irregular lignified cells over the healed scars. Thus the closure of the branch scars is essentially similar to the wound healing mechanism described by Zimmermann & Brown (1971). A number of abscission scars are healed every year. The tubercular structures thus formed grow irregularly and appear gall-like and in sectional view show numerous healed scars, as the one shown in Fig. 12, oriented in various planes. The xylem tissue is irregularly aligned over and around the scars.

Summer leaf shedding in the tropics, where differences in photoperiod are less pronounced, is generally held to be associated with drought resistance (Kozlowski, 1973; Addicott, 1978). Natural shedding of leaves and other parts reduces transpiring surface area and prevents dehydration of plants to lethal levels

(Kozlowski, 1973). Moisture stress influences the abscission of leaves, buds, flowers and young fruits in many crop plants (Addicott & Lyon, 1973). It has also been found that shortage of water enhances shoot tip abscission in *Tilia cordata* Mill. seedlings (Pigott, 1984). In *L. microcarpa* also it is observed that trees growing in moist sites retain their leaves for a longer period. Branch abscission is regarded as a close parallel to leaf abscission, being involved in reduction of transpiring surface (Orshan, 1954). Branch shedding in *L. microcarpa* appears to be comparatively less specialised abscission. However, seasonal production of leafy shoots and abscission of their dry twigs during the unfavourable part of the year does not appear to be a mere 'self-cleaning mechanism' but rather an efficient method of water conservation.

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