THE ANATOMY OF THE BARK OF AGATHIS IN NEW ZEALAND

by

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Summary

The anatomy of the bark of *Agathis australis*, which is indigenous to New Zealand, is described. The phloem cell types include sieve cells, axial and ray parenchyma, fibres and sclereids. Resin canals are found in the primary cortex, phloem and phelloderm. Large crystals are found in the lumina of some sieve cells and axial parenchyma cells, while minute crystals (crystal sand) are observed in the walls of phelloderm cells and complementary tissue cells. The primary cortex persists on the stem for a long time. The shape of phellem and phelloderm cells cut off by phellogen derived from cortical cells are different from those cut off by phellogen derived from phloem parenchyma cells. A trabecula was observed in a radial row of phellem cells.

Key words: *Agathis*, bark anatomy, crystals, resin canals, trabecula.

Introduction

Only one species of *Agathis* (Araucariaceae) occurs naturally in New Zealand, namely *A. australis*. The other species of the genus are distributed in Australia, New Caledonia, Fiji, Philippines, and the Malay Peninsula (Dallimore & Jackson, 1966). *Agathis australis*, which is endemic to New Zealand, is a tall tree up to 30 m high (rarely up to 60 m) with a trunk up to 3 m diameter, occasionally up to 7 m. It is found in lowland forests in the North Island from near North Cape to latitude 38° S (Allan, 1961).

Patel (1968) studied the anatomy of the wood of *A. australis* using optical microscopy while Meylan and Butterfield (1978) employed scanning electron microscopy in their work on the same wood. However, little is known about the anatomy of the bark of *A. australis*. Robinson and Grigor (1963) studied the origin of the periderm in some New Zealand plants which included *A. australis*. In presenting a biological description of *A. australis*, Ecroyd (1982) gave very scanty information on the anatomy of the bark. This information was obtained when the present study was still in a preliminary stage.

All the terms used in this paper follow those in an earlier paper (Chan, 1985).

Materials and Methods

Three trees were selected from Puketi State Forest while a fourth tree came from the garden of the Staff Club of the University of Canterbury, Christchurch, New Zealand. Two samples of the bark were collected at breast height from opposite sides of each tree.

Methods of fixation, preparation and examination of the specimens follow those in an earlier paper (Chan, 1985).

Descriptions

The diameters at breast height of the trees were 64.8, 154, 119.5 and 34.8 cm and the thicknesses of the living bark at the same height were 1.4, 2.3, 2 and 1 cm respectively.

The phloem comprises sieve cells, axial and ray parenchyma, fibres and sclereids. Resin canals are also present (Figs. 1A, B; 2A, B). Sieve cells, axial parenchyma and fibres appear randomly arranged (Fig. 4A). The conducting phloem seems to be about 1–1.3 mm wide. Sclereids and resin canals begin to be formed (Fig. 1A) in the region where the phloem ceases its conduction activity. Sclereids occur in irregular radial rows while resin canals tend to occur in tangential rows (Fig. 5C).

In the active zone sieve cells appear rectangular in transverse section (TS). Large crystals (> 20 µm long), mostly hexagonal prismatic in shape, occur in some sieve cells in the non-conducting phloem. Most sieve cells are crushed by sclereids in this region (Fig. 1A, B). Sieve areas are about 8–18 µm in diameter, mostly in the radial walls in single files (Fig. 4B).

Axial parenchyma cells are isodiametric in TS and rectangular in radial longitudinal section (RLS) and tangential longitudinal section (TLS). In the immediate proximity of the vascular cambium, the phloem parenchyma mother cell divides, often forming walls in the radial longitudinal plane (Fig. 4A, C) and also in the

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transverse plane, thus giving rise to two adjacent strands of parenchyma cells that are ontogenetically related. Sometimes the transverse wall is laid down obliquely producing parenchyma cells that initially appear abnormally-shaped (Fig. 4C) but later seem to attain the normal shape. Some parenchyma cells are filled with tannin while others possess large crystals ($> 20 \mu\text{m}$ long), mostly hexagonal prismatic in shape (Fig. 4D). In the non-conducting phloem, some parenchyma cells (especially those without tannin contents) develop into sclereids, growing to many times the original size (Fig. 1A, B, 2A, B). In the outer part of the non-conducting phloem, the non-sclerified parenchyma cells are almost isodiametric in all planes (Fig. 4E).

Phloem rays are uniseriate, occasionally partly biseriate, usually 2–16 cells high (total range 1–27). The cells are round in TLS near the vascular cambium (Fig. 4C), rectangular in TS and rectangular to slightly rhombic in RLS. Towards the outer part of the non-conducting phloem, most of the phloem ray cells become slightly elliptical in TLS, some dilating extensively (Fig. 3B), appearing slightly elongated in the horizontal tangential direction or isodiametric in all planes. In the non-conducting phloem, some ray cells sclerify, growing irregularly to many times their original size.

Fibres are rectangular to round in TS (Fig. 4A). Their walls are birefringent and thick but are not stained by safranin. However, some fibres in the outer part of the non-conducting phloem have lignified walls, especially those immediately adjacent to sclereids. The lumina of fibres are small and almost indistinct. The wall is made up of three main layers: two very thin layers on the outside and one very thick layer on the inside (Fig. 5A, B). On drying, the innermost layer seems to undergo greater shrinkage than the outer layers (Fig. 5B).

Phloem sclereids are very abundant (Fig. 1A, B, 2A, B). They have irregular shapes but tend to be slightly elongated, oriented in the longitudinal direction. Sclereid walls are polylamellate, lignified and birefringent. Most sclereids have large empty lumina (Fig. 1A, B; 2A, B; 3A, B; 4E).

Phloem resin canals are found only in the non-conducting phloem. In regions where a resin canal is destined to be formed, the axial and ray parenchyma cells divide repeatedly (Fig. 5E). Eventually, the cells in the centre undergo lysis forming a canal about $175\text{--}200 \mu\text{m}$ in diameter (Fig. 5D). Phloem resin canals are oriented axially, and tend to occur in tangential rows; they do not seem to anastomose with each other. Canals within each tangential row are spaced about $375 \mu\text{m}$ or greater apart.

The primary cortex seems to persist for a long time on the stem. Cortical cells appear isodiametric to rectangular (with long axes in the tangential direction) in TS and TLS, and isodiametric in RLS. Resin canals which seem to be lysigenous in origin, about $100\text{--}250 \mu\text{m}$ in diameter, are found randomly in the cortex, traversing in the axial direction and do not seem to anastomose. Some of the cortical cells are sclerified, mostly with large empty lumina (Fig. 5F), expanding to only a few times the original size. Cortical sclereids tend to occur as tangential bands or groups.

The periderm consists of about 45–65 layers of phellogen, one layer of phellogen and about 25–35 layers of phelloderm. In 'younger stems' (probably $< 80 \text{ cm}$ diameter), where the cortex is still present, the phellogen is derived from cortical cells while in 'older stems' (probably $> 100 \text{ cm}$ diameter), the phellogen arises in the phloem.

Phelloderm cells in 'younger stems' (i.e., those produced by phellogen derived from cortical cells) appear rather narrowly rectangular in TS (Fig. 6A) and TLS (with long axes in the tangential horizontal direction) and isodiametric in RLS (Fig. 6B, C). The first 2–4 layers of cells closest to the phellogen have thin walls (Fig. 6B) and tannin contents (Fig. 6D). Later, the walls, except for the end walls, become thickened but neither lignified nor polylamellate (Fig. 6C, D). Eventually, only very few phelloderm cells contain tannin. Some phelloderm cells develop into sclereids (Fig. 6E), growing irregularly to a few times larger than the original cells (Fig. 6F), mostly with large empty lumina. Other phelloderm cells expand without sclerification becoming rectangular to isodiametric in all planes, resembling cortical cells. Sometimes phelloderm cells can only be distinguished from cortical cells by the ordered radial rows of the former. Resin canals, which seem to be lysigenous in origin, about $100\text{--}150 \mu\text{m}$ in diameter, occur randomly in the phelloderm (Fig. 6D). They traverse in the axial, horizontal and inclined directions and some of them form anastomoses, the horizontal branches being more common.

Phelloderm cells in 'older stems' (i.e., those produced by phellogen derived from phloem parenchyma) appear slightly rectangular or square to isodiametric in TS and RLS, and 4–6-sided in TLS. The first 3–5 layers of cells closest to the phellogen are all thin-walled and filled with tannin. Later, some of the cells sclerify and grow to a few times their original size, with large lumina (Fig. 3B) while others undergo expansion only. In either case, the

(text continued on page 239)

Legends to Figures 1–7 (all Agathis australis bark):

Fig. 1 & 2. General view of the inner part of the living bark; TS (LM), x 50. Top of Fig. 1A joins bottom of 1B, top of 1B joins bottom of 2A and top of 2A joins bottom of 2B. Vascular cambial region just beyond bottom edge of 1A. Sclereids with large empty lumina (Sc); resin canals (Rc); rays (R-r). Unlabelled arrow in 1A indicates approximately the boundary between the conducting and non-conducting phloem; note that sclereids begin to appear only in the non-conducting phloem and that sieve cells are all crushed in this region.

Fig. 3. General view of the outer part of the living bark; TS (LM), x 50. Top of Fig. 3A joins bottom of 3B. Sclereids with large empty lumina (Sc); resin canal (Rc); rays (R-r); expanded phloem parenchyma cells (E); phelloderm (D); phellem (M). Ray in 3B has dilated (unlabelled arrow). Primary cortex absent in this specimen.

Fig. 4. A: Conducting phloem showing randomly scattered arrangement of cells; TS (LM), x 130. Ray (R-R'); sieve cells (S); ordinary axial parenchyma cells (P, with dark tannin contents); axial parenchyma cells with walls laid in the radial longitudinal plane (unlabelled arrows); fibres (F) with rectangular to round shapes. — B: Sieve areas on the radial wall in a single file; RLS (SEM), x 980. — C: Dividing axial parenchyma mother cells (P) near the vascular cambium; TLS (SEM), x 250. Radial longitudinal walls dividing the mother cells into two strands (unlabelled arrows); end wall of cell on right laid down obliquely (O). Note the round shape of ray cells (r). Sieve cells (S). — D: Crystals (X) in axial parenchyma cells; RLS (LM), x 270. — E: Phloem sclereids (S) with large lumina and polyamellate walls, and isodiametrically shaped non-sclerified parenchyma cells (N); RLS (SEM), x 870.

Fig. 5. A: Fibre wall showing three layers; two outer thin layers (1, 2) and one inner thick layer (3); Ray cells (R); TLS (SEM), x 2,500. — B: Fibres showing that the inner layer (3) undergoes greater shrinkage than the outer layers (1, 2); Sclereid (Sc); TS (SEM), x 1,040. — C: Low power view of the phloem, showing the tangential rows (arrows) of resin canals; TS (SEM), x 10. — D: A phloem resin canal (Rc); Epithelial cells (E); Parenchyma cells (p); TLS (SEM), x 96. — E: A developing phloem resin canal showing dividing parenchyma cells (arrows) with two fibres (f) among them; Ray (R-r); TS (LM), x 110. — F: Cortical sclereids (S) showing polyamellate walls and large distinct lumina; Non-sclerified cortical cell (N); RLS (SEM), x 900.

Fig. 6. A: Periderm whose phellogen is derived from cortical cells, showing the narrowly rectangular phelloderm (D) and phellem cells (M); TS (LM), x 250. Note that the phellogen has undergone an anticlinal division (arrow). — B: Periderm whose phellogen is derived from cortical cells showing rectangular phellem cells (M) and isodiametric phelloderm cells (D) with thin walls; RLS (SEM), x 920. — C: Phelloderm cells with thickened walls (produced by phellogen derived from cortical cells); RLS (SEM), x 920. Note the isodiametric shape. — D: Early stage of development of a resin canal (R) in the phelloderm produced by phellogen derived from cortical cells; RLS (LM), x 250. Thin-walled phelloderm cells (T) close to the phellogen with tannin contents; thick-walled phelloderm cells (TH) away from the phellogen. — E: Thick-walled phelloderm showing a cell developing a sclerified wall (S); RLS (SEM), x 520. — F: Macerated phelloderm sclereids showing their irregular shape; (LM), x 50.

Fig. 7. A: Crystals (arrow) between phelloderm cells of lenticels; RLS (SEM), x 890. — B: A lenticel (under polarised light) showing birefringent crystals in the phelloderm (D) and the complementary tissue (Ct); Phellogen (N); Phellem (M); TS (LM), x 30. — C: Phellem cells produced by a phellogen derived from cortical cells, showing their narrow rectangular to irregular oblong shape; TLS (SEM), x 470. — D: Phellem cells produced by a phellogen derived from phloem parenchyma cells, showing their irregular polygonal shape; TLS (LM), x 250. — E: Phellem cells produced by a phellogen derived from phloem parenchyma cells; TS (SEM), x 430. Note that the walls of the inner cells (I) are thicker than those of the outer cells (O). — F: Thin-walled phellem cells showing that the inner tangential wall (I) is slightly thicker than the outer tangential wall (O) and that the tangential wall is thicker than the radial wall; TS (SEM), x 2,400.

Fig. 8. *Agathis australis* bark. — A: Two outermost layers of phellem cells exhibiting thick non-polylamellate walls, appearing rectangular in shape (K); Thin-walled phellem cells (G); TS (LM), x 510. — B: A trabecula (arrows) in phellem cells, traversing from one tangential wall to the next; TS (SEM), x 950. Note the twist in the trabecula.

cells appear isodiametric in all three planes. Eventually, only some of the phelloderm cells retain their tannin contents. Resin canals, which seem to be lysisogenous in origin, are plentiful in the phelloderm, occurring just adjacent to the phloem in one or two tangential rows. They have a diameter of c. 50–70 μm and traverse in the axial, horizontal and inclined directions, forming anastomoses within each tangential row.

Minute crystals (< 8 μm long), mostly hexagonal prismatic in shape, occur commonly in the cell wall of phelloderm cells in the region of the middle lamella. Very high accumulation of such crystals can be found especially in the wall of phelloderm cells of lenticels (Fig. 7A, B).

Phellem cells in 'younger stems' appear narrow rectangular to irregular oblong in TS and TLS (with long axes in the tangential horizontal direction) (Figs. 6A, 7C) and rectangular in RLS (Fig. 6B). The inner 42–64 layers of phellem cells in 'older stems' appear narrowly rectangular in TS and RLS and irregularly polygonal in TLS (Fig. 7D). In both cases, the walls are generally thin, though sometimes they may vary in thickness, the outer cells exhibiting slightly thinner walls (Fig. 7E). Furthermore, the tangential wall is usually thicker than the transverse and radial walls, and the inner tangential wall tending to be slightly thicker than the outer tangential wall (Fig. 7F). The outer 1–3 layers of phellem cells in 'older stems' are thick-walled, appearing rectangular to square in TS (Fig. 8A) and RLS, and 4–6-sided in TLS and are larger in size than the cells of the inner layers. The walls of such thick-walled phellem

cells seem slightly lignified (slightly stained with safranin) and birefringent but not poly-lamellate. Phellem cells are mostly without contents but some of them, in short tangential rows, are filled with tannin.

The complementary tissue cells of lenticels show high accumulation of minute crystals (< 8 μm long) (Fig. 7B), mostly hexagonal prismatic in shape, occurring in the cell wall in the region of the middle lamella.

A trabecula was observed in one specimen in a radial row of phellem cells, traversing in the radial direction from one tangential wall to the next. The trabecula was not a normal straight rod but appeared as a twisted rod within each phellem cell (Fig. 8B).

Discussion

The phloem cell types in *Agathis australis* are, unlike most of the other New Zealand gymnosperms, not arranged in regular rows (Chan, 1979, 1982, 1985). However, the resin canals tend to be in tangential rows.

The large hexagonal prismatic crystals (> 20 μm long) found in the lumina of some sieve cells in *A. australis* have been reported in sieve cells previously. Chang (1954b) found them in *Pinus elliotii*, but Esau (1969) questioned the observation, suggesting that it was a misinterpretation of crystalliferous parenchyma cells as sieve cells. Howard (1971) also noted the same phenomenon in the barks of U.S. southern pines, including *P. elliotii*. Both Chang (1954b) and Howard (1971) reported the crystals to be styloid in shape unlike those in *Agathis australis*.

Large hexagonal prismatic crystals ($> 20 \mu\text{m}$ long) are also found in the lumina of some axial parenchyma cells. Occurrence of crystals in the phloem parenchyma cells is commonly reported in many species (Strasburger, 1891; Chang, 1954a, b; Bamber, 1962; Srivastava, 1963a, b; Esau, 1969; Howard, 1971, 1977; Barnett, 1974; Patel, 1975; Bramhall & Kellogg, 1979; Chan, 1979, 1982).

The formation of walls by phloem axial parenchyma mother cells in the radial longitudinal plane and transverse or oblique-transverse plane, giving rise to two strands of axial parenchyma cells that are ontogenetically related as occurs in *A. australis*, has also been observed in *Dacrydium biforme* and *D. cupressinum* (Chan, 1982) but does not seem to have been reported elsewhere.

One unusual feature of phloem fibres of *Agathis australis* is that their walls are not stained by safranin. Another interesting observation is that upon drying, the innermost layer of the fibre wall undergoes greater shrinkage than the two outer layers. In these respects they resemble gelatinous xylem fibres (cf. Butterfield & Meylan, 1980). For *Agathis* further study is necessary to ascertain whether the phloem fibres have proper G-layers. Sclereids are found in the phloem, primary cortex and phelloderm and all have large empty lumina.

Robinson and Grigor (1963) described the origin of the first periderm in *Agathis australis* as sub-epidermal. This seems to agree with the findings of the present study. In the smaller stems examined (64.8 and 34.8 cm diameter), the primary cortex was still present and the periderm must have been developed from cortical cells, although it is uncertain as to whether this periderm was the first or not. It is clear that very few subsequent periderms or none at all are formed for a very long time after the formation of the first periderm. Yet Allan (1961) described the bark of *A. australis* as falling in large thick flakes. Hinds and Reid (1957) also noted that large mounds of shed bark accumulate at the base of the trunk. The most plausible explanation is that once the primary cortex has been completely exfoliated and the periderm is derived from phloem parenchyma cells, the frequency of formation of successive periderms increases, leading to accumulation of exfoliated bark.

Phelloderm and phellem cells in 'younger stems' (i.e., those produced by phellogen derived from cortical cells) appear rather narrowly rectangular to irregular oblong in TS and TLS, with their long axes in the tangential horizontal direction. It can be explained that this phellogen which was formed when the stem was

still very small in diameter has been 'stretched', giving rise to such long cells, although it would be expected that anticlinal divisions do take place from time to time to keep up with the increasing circumference (Fig. 6A).

Apart from the differences in shapes, phelloderm in 'younger stems' differ in one other aspect from phelloderm in 'older stems' (i.e., those produced by phellogen derived from phloem parenchyma cells). In the former, the first 2–4 layers of phelloderm cells closest to the phellogen have thin walls which eventually develop into thick walls before some of the cells become sclereids. In the latter, the cells remain thin-walled throughout, with some of the cells also becoming sclereids.

Another difference between phellem cells in 'younger stems' and phellem cells in 'older stems' is that in the latter, the outer 1–3 layers of cells have thick, slightly lignified, birefringent but nonpolylamellate walls.

The presence of resin canals is a prominent feature of the bark of *A. australis* as they are found in the phloem, primary cortex and phelloderm. The resinous nature of the bark of *A. australis* is well-known. Hinds and Reid (1957) mentioned that in mature trees, the massive branches are impregnated with resin and also that other inflammable organic material collect at the base of the trunk together with large mounds of shed bark. The occurrence of resin canals in phelloderm has to my knowledge never been recorded before. Resin canals in the phelloderm of 'older stems' and those in the phloem are arranged in tangential rows while those in the phelloderm of 'younger stems' and primary cortex are distributed randomly. In the phloem and primary cortex, the resin canals traverse only in the axial direction and do not form anastomoses. In the phelloderm of both 'younger and older stems', resin canals traverse in the axial, horizontal and inclined directions, forming anastomoses. In 'younger stems', the anastomoses are formed only within each tangential row. Resin canals are largest in diameter in the primary cortex (100–250 μm), second largest in the phloem (175–200 μm), followed by those in the phelloderm of 'younger stems' (100–150 μm) and those in the phelloderm of 'older stems' (50–70 μm).

Minute crystals ($< 8 \mu\text{m}$ long), mostly hexagonal prismatic in shape, are commonly found in the wall of phelloderm cells of *A. australis* but are not detected in the wall of the phellem cells. However, they are found in great abundance in the wall of complementary tissue cells and phelloderm cells of lenticels. Chan (1982) noted that minute crystals are in greater abundance in the wall of phelloderm cells of lenti-

cells than in normal phelloderm cells in *Dacrydium intermedium*, *D. colensoi*, *Phyllocladus alpinus*, *P. glaucus* and *P. trichomanoides*. He further reported that minute crystals are only found in the wall of phelloderm cells of lenticels in *Dacrydium kirkii*, *D. bifforme* and *D. bidwillii* but not in the wall of normal phelloderm cells. The occurrence of crystals in the walls of complementary tissue cells has not been recorded before. The presence of such crystals in the region of the lenticels may indicate that formation of crystals is related to gaseous exchange, which is believed to be the function of lenticels (Cutter, 1969).

The occurrence of trabeculae in phellem cells has not been noted elsewhere. Neither Patel (1968) nor Meylan and Butterfield (1978) made any mention of trabeculae in the wood of *Agathis australis*. There are two possible explanations of the origin of trabeculae in phellem cells. A trabecula is either formed directly in the phellogen cell which then cuts off phellem cells with trabeculae or it is first formed in the vascular cambium which then cuts off phloem cells with trabeculae. Later, one of the parenchyma derivatives becomes a phellogen cell, thereafter giving rise to phellem cells with trabeculae. In the present study it could not be determined which is the more plausible explanation, because during specimen preparation, the trabecula was cut off, so that it could not be traced to the phellogen or vascular cambium.

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