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Cell walls in oil and mucilage cells*

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SUMMARY

The development and ultrastructure of cell walls of oil and mucilage cells in selected representatives of so-called primitive and derived dicotyledons are summarized, and compared with information on cell walls in other idioblasts and secretory or protective tissues. Oil and mucilage cells of *Cinnamomum* and *Annona*, and presumably other Laurales and Magnoliales, are both characterized by a suberized layer deposited against the primary wall. These taxa usually do not form mucilage or oil cavities through fusion of secretory cells. *Hibiscus* and other Malvales lack such a suberized layer in their mucilage cells and as a rule have mucilage cavities, resulting from the breakdown of common walls between mucilage cells.

The inner, polysaccharide wall deposited against the suberized wall layer in oil cells strongly resembles the first deposited, dense mucilage layer in mucilage cells; the precise composition of these wall layers requires further study.

It is hypothesized that, as in certain crystalliferous cells, laticifers, secretory trichomes, and epithelial cells of resin ducts, the suberized layer in oil and mucilage cells serves to compartmentalize the secretion product. In evolution the suberized layer may have been lost in mucilage cells in plant groups which possess exclusively mucilaginous secretory elements, and which are derived from ancestors with oil cells. However, an independent, *de novo* (parallel) origin of mucilage cells (and cavities) without suberized wall layers in derived and often unrelated dicotyledonous families may have been an alternative evolutionary pathway.

Key-words: cell wall, mucilage cell, oil cell, plasmodesma, suberized layer.

INTRODUCTION

Oil and mucilage idioblasts are specialized solitary cells that synthesize and store oil and mucilage respectively (Metcalfe 1983; Chalk 1983). Although these two types of idioblasts are quite different at maturity, ultrastructural studies on oil and mucilage cells in primitive dicotyledons revealed that these two cell types share a number of identical features (Bakker *et al.* 1991). The old idea about the mutual replacement of mucilage cells by oil

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cells (Janssonius 1926, 1934), revived by the recent hypothesis of a possible homology between oil and mucilage cells (Baas & Gregory 1985; Gregory & Baas 1989) was thereby further strengthened. One of the most important similarities of the oil and mucilage cells in so-called primitive dicotyledonous Magnoliales and Laurales is the presence of a suberized layer in the cell wall (Bakker & Gerritsen 1989, 1990; Bakker *et al.* 1991). Previously only oil cells were said to be characterized by a suberized layer in their cell wall (for review see: Baas & Gregory 1985).

On the other hand mucilage cells in, for example, the Malvales, possess a general mucilage cell type which lacks a suberized layer (see Gregory & Baas 1989; Bakker & Gerritsen 1992).

In this paper, ultrastructural features of the cell-wall development of oil and mucilage cells in the above-mentioned taxa will be surveyed and the possible biological function of the suberized layer in idioblasts will be discussed in relation to other secretory structures. Furthermore, the evolution of oil and mucilage cells will be discussed.

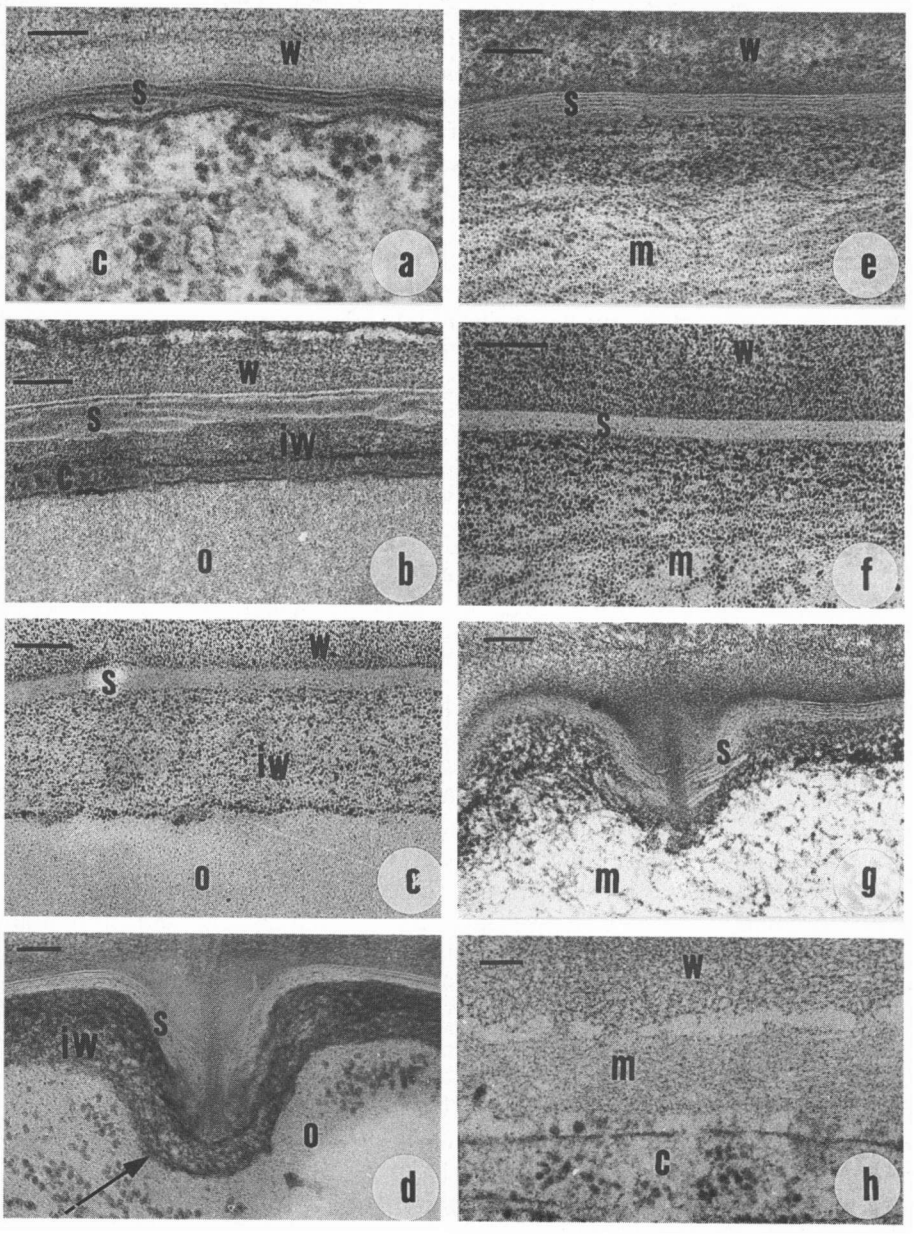
The materials and methods are described in detail in Bakker & Gerritsen (1989, 1990, 1992) and Bakker *et al.* (1991).

SURVEY OF CELL-WALL DEVELOPMENT IN OIL AND MUCILAGE CELLS

Oil and mucilage cells in Cinnamomum *(Lauraceae) and* Annona *(Annonaceae)*

Early in the development of both oil and mucilage cells, before the onset of oil or mucilage deposition, a suberized layer is deposited on the inner side of the cell against the primary wall. The suberized layer is composed of alternating light and dark lamellae, which show up in osmium-fixed material (Fig. 1a,b). First, the suberized wall layer is composed of a few lamellae (Fig. 1a), but later in development several lamellae (up to *c.* 10) can be distinguished, which become more or less indistinct with maturity of the oil (Fig. 1b) or mucilage cell (Fig. 1e). When the material was not postfixed with osmium, but stained with the Thiéry silver staining procedure (1967) the lamellae could not be visualized (Fig. 1c,f).

Fig. 1. Details of the cell wall of a future idioblast (a), mature oil cells (b–d) and mucilage cells (e–h). TEM. Bar = 0·1 μm. Abbreviations used: c, cytoplasm; iw, inner wall layer; m, mucilage; o, oil cavity; s, suberized wall layer; w, primary wall. (a) *Annona muricata.* Detail of the cell wall in a future idioblast before the secretory stage, showing the suberized wall layer deposited against the primary cell wall. Several lamellae of the suberized wall layer are visible shortly before the onset of the secretory stage. (b) *A. muricata.* Detail of the typically three-layered cell wall of a mature oil cell. The lamellae of the suberized layer are less distinct than in the preceding stages. The inner wall layer is densely stained. A thin cytoplasmic layer is present between the oil cavity and the inner wall layer. (c) *Cinnamomum verum.* Detail of the cell wall of a mature oil cell fixed without osmium tetroxide and stained with the Thiéry silver solution. The suberized layer does not show any lamellation or staining, while the primary cell wall and the inner wall layer are stained distinctly. (d) *Cinnamomum burmanni.* Detail of a typical plasmodesma in the cell wall of a mature oil cell. Note the typical bulge of the primary wall on the idioblast side. This structure is not occluded by the suberized wall layer. The inner wall layer completely covers this structure (arrow). The oil cavity completely fills the cell lumen and the cytoplasm has disappeared. (e) *C. burmanni.* Detail of the cell wall in a near-mature mucilage cell. The suberized layer is deposited against the primary cell wall. Subsequently mucilage is deposited against the suberized layer. Note that the first zone of deposited mucilage (directly underneath the suberized wall layer) is more densely stained and more compact than the later deposited mucilage. (f) *C. burmanni.* Detail of the cell wall in a mature mucilage cell fixed without osmium tetroxide and subsequently treated with the silver solution. Note the unstained suberized layer sandwiched between the stained primary cell wall and the deposited mucilage. (g) *C. burmanni.* Detail of a typical plasmodesma in the cell wall of a mature mucilage cell showing a typical bulge on the idioblast side. The plasmodesma is not occluded by the suberized layer, but later deposited mucilage will cover this structure. (h) *Hibiscus schizopetalus.* Detail of the cell wall of a young mucilage cell. Note that the mucilage is deposited directly against the primary cell wall. A suberized wall layer is absent in the mucilage cells.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In the oil cells an additional wall layer is deposited against the suberized layer: the inner wall layer. The thickness of this layer increases in thickness with development and varies between the plant species (compare Figs 1b and 1c). The inner wall layer stains after fixation with Karnovsky fixative followed by osmium tetroxide (Fig. 1b) and with the Thiéry silver staining procedure (see Bakker & Gerritsen 1989) (Fig. 1c). In the cell walls of mature oil cells typical plasmodesmata occur, characterized by a bulge on the idioblast side (Fig. 1d). These are not covered by the suberized layer. However, the later deposited inner wall layer completely covers the plasmodesmata (Fig. 1d).

In mucilage cells the cell wall has a two-layered appearance composed of the primary wall and a suberized layer. The suberized layer develops in an identical way to that in oil cells (Fig. 1e). Mucilage is deposited against the suberized layer (Fig. 1e,f) and stains with the conventional fixation procedure (Fig. 1e) and more specifically with the Thiéry silver staining method (Fig. 1f). The first zone of deposited mucilage is more compact and stains more densely than the later secreted mucilage (Fig. 1e). Typical plasmodesmata are also present in the cell wall of the mucilage cells (Fig. 1g). These structures are not covered by the suberized wall layer, but finally become occluded by mucilage (Fig. 1g).

Mucilage cells in Hibiscus schizopetalus

The developmental sequence of the mucilage cells of *Hibiscus* is very similar to that of the mucilage cells of *Cinnamomum* and *Annona* (Bakker & Gerritsen 1992). However, the mucilage cells in *Hibiscus* never possess a suberized wall layer (Fig. 1h). The mucilage is deposited directly against the primary wall (Fig. 1h). The mucilage cells develop in pairs or larger groups. At maturity their common cell walls disintegrate and thus constitute mucilage cavities with a continuous mucilage mass. These cavities are sheathed by smaller elongated cells (Bakker & Gerritsen 1992).

DISCUSSION

More than a century ago Zacharias (1879) had already noticed the presence of a suberized layer in various secretory plant structures including oil and mucilage cells. The presence of a suberized layer is generally accepted as being typical for oil cells (Müller 1905; Lehmann 1925; Leemann 1928; Ziegler 1960; Ricci 1953, 1966; Scott *et al.* 1963; Amelunxen & Gronau 1969; Wattendorff 1974b; Maron & Fahn 1979; Platt-Aloia *et al.* 1983; Fineran *et al.* 1988; Mariani *et al.* 1989). This wall layer has also been examined ultrastructurally in a number of other secretory structures. Crystal-containing idioblasts possess a suberized layer surrounding the crystal (Wattendorff 1976a,b; Espelie *et al.* 1982; Parameswaran & Richter 1984) which in one species (*Larix decidua* Mill.; Wattendorf 1969) continues into the cell wall. In oil or mucilage secreting trichomes a suberized layer has been found between the head and the stalk (Kristen 1974; Thomson *et al.* 1979; Bruni & Modenesi 1983). In salt glands a kind of suberized layer is present in the anticlinal walls of the secretory cells in the head (Bosabalidis & Thomson 1984). A suberized layer has recently been found in the wall of laticifers (Fineran *et al.* 1988; Condon & Fineran 1989) and in the outer walls of the epithelial cells of resin ducts (LaPasha & Wheeler 1990).

Several functions have been attributed to the presence of suberin in plant structures. It can act as a barrier to water loss (Botha *et al.* 1982), to fungal attack (Newcombe & Robb 1989; Brett & Waldron 1990), against cold stress, or serve for compartmentalization (Kolattukudy 1984; Kolattukudy & Espelie 1989). The latter function can be assumed for oil and mucilage cells: the suberized layer functions as a barrier to prevent leakage of

potentially toxic substances from the idioblasts into the surrounding cells (Ricci 1966; Espelie *et al.* 1982; Platt-Aloia *et al.* 1983; Kolattukudy 1984; Kolattukudy & Espelie 1989; Bakker & Gerritsen 1989, 1990; Bakker *et al.* 1991). Furthermore, a suberized layer blocks the apoplastic transport between the cells. The idioblast is sealed off from the surrounding cells.

As the mucilage cells of *Hibiscus schizopetalus* generally lack a suberized wall layer (Bakker & Gerritsen 1992) the absence of a suberized layer may be related to the appearance of mucilage cavities and canals, a characteristic frequently occurring in the Malvaceae, Tiliaceae and Sterculiaceae (Bouchet 1971, 1973; Bouchet & Deysson 1974, 1976). The mucilage cells in *Cinnamomum* (Lauraceae) and *Annona* (Annonaceae), that possess a suberized wall layer, show the solitary cell type in which local cell wall breakdown has been observed only sporadically (Bakker & Gerritsen 1990, 1992; Bakker *et al.* 1991).

The inner wall layer in oil cells stained distinctly with the Thiéry staining solution (Fig. 1e), thus indicating a polysaccharide nature. Several other plant structures, containing a suberized layer in the cell wall, also deposit an additional wall layer, which shows some similarity with the inner wall in oil cells (e.g. cork cells: Sitte 1962; Wattendorff 1974a,b; pitcher hypodermis: Joel & Heide-Jørgensen 1985; laticifers: Fineran *et al.* 1988; Condon & Fineran 1989).

The first zone of deposited mucilage in mucilage cells of *Cinnamomum* (Fig. 1d) resembles the inner wall layer in oil cells (Fig. 1c). Both layers are composed of polysaccharides, as was demonstrated with the Thiéry staining method (Fig. 1e,f) but cytochemical/biochemical studies are needed to analyse the precise composition of these two wall 'layers'. Specific labels, such as enzymes, lectins, polyclonal or monoclonal antibodies can be applied to detect specific cell-wall polysaccharides, such as cellulose, glucans, galacturonans and pectins (Knox 1992; McCann *et al.* 1992; Vian *et al.* 1992).

The plasmodesmata in both oil and mucilage cells of *Cinnamomum* and *Annona* show a bulge on the idioblast side of the cell wall (Fig. 1d,g). Identical structures have been observed in other oil cells (Maron & Fahn 1979; Platt-Aloia *et al.* 1983). The plasmodesmata are not occluded by the suberized layer (Fig. 1d,g). In other plant tissues plasmodesmata have also been reported to penetrate the suberized wall layer (Joel & Heide-Jørgensen 1985; Clarkson *et al.* 1987; Condon & Fineran 1989; Schmitt & Liese 1991).

At full maturity the inner wall layer or the mucilage covers the plasmodesmata. As a consequence, the symplastic pathway of transport between cells is blocked by the deposition of the inner wall layer in oil cells (Fig. 1d) or with the mucilage deposition in mucilage cells (Fig. 1g). Thus both the apoplastic and symplastic transport are presumably blocked finally.

One can only speculate on the function of a suberized layer in the mucilage cells of primitive dicotyledons, as exemplified by the Lauraceae and Annonaceae (Bakker & Gerritsen 1989 1990; Bakker *et al.* 1991). However, it can be hypothesized that the mucilage cells in the primitive plant groups (as in Lauraceae and Annonaceae) presumably inherited the ability to deposit a suberized layer from the originally occurring oil cells, which always deposit a protective suberized layer. The presence of a suberized layer in the mucilage cells can thus be considered to be an ancestral remnant, without a function in the new secretory cell type. The more advanced dicotyledons may subsequently have lost the ability to deposit a suberized layer in mucilage cells during their evolution and so the mucilage cell type in, for example, the Malvaceae, developed. From these mucilage cells,

lacking a suberized wall layer, mucilage cavities and canals could develop. Fahn (1988a,b) proposed an evolutionary developmental trend for secretory structures in plants: internal solitary idioblasts would have developed into secretory cavities, canals and ducts, and finally external secretory structures such as trichomes would have developed. A classification of terpenoid secreting plant structures was based on identical criteria (Denisova 1975). All above hypotheses assume that internal secretory structures are somehow derived from each other in evolutionary lineages. It is, of course, also possible that mucilage cells without a suberized wall layer arose '*de novo*' in parallel development, several times in the evolution of dicotyledons. Their distribution over a wide range of unrelated families (Gregory & Baas 1989) could be cited in favour of this alternative hypothesis.

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