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CUTICLE DEVELOPMENT ON GLANDULAR TRICHOMES OF CANNABIS SATIVA (CANNABACEAE)[1]

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The dermal sheath of glandular trichomes of *Cannabis sativa* L., consisting of cuticle and a subcuticular wall, was examined by transmission electron microscopy. Cuticle thickened selectively on the outer wall of disc cells of each trichome prior to formation of the secretory cavity, whereas thickening was less evident on the dermal cells of the bract. Membraned secretory vesicles that differ in size and appearance in the secretory cavity were the source of precursors for synthesis of cuticle. Vesicle contents, released following the degradation of the vesicle membrane upon contact with the subcuticular wall, contributed to both structured and amorphous phases of cuticle development. The structured phase was represented by deposition and thickening of cuticle at the subcuticular wall-cuticle interface to form a thickened cuticle. In the amorphous phase precursors permeated the cuticle in a liquid state, as shown by fusion of cuticles and wax layers between contiguous glands, and may have contributed to growth in surface area of the expanding sheath. Disc cells are interpreted to control growth of secretory cavity by secretion of membraned vesicles into the cavity. The thickened cuticle, which increased eightfold in thickness during enlargement of the gland, provided structural strength for the extensive surface area of the dermal sheath. The gland of *Cannabis* in which vesicle contents contribute to the growth in thickness and surface area of the cuticle of the sheath is interpreted to represent a phylogenetically derived state as contrasted to secretory glands possessing only cuticle and lacking a complement of secretory vesicles.

The cuticle forms a continuous layer over the surface of the shoot including dermal features such as trichomes. The structure and chemistry of cuticle on the surface of dermal cells in particular have been studied and reviewed (Martin and Juniper, 1970; Cutler, Alvin, and Price, 1982; Juniper and Southwood, 1986). Considerable progress on structure and organization of cuticle on the surface of dermal cells is described in these reports, but cuticle structure, development, and significance on other cell types (such as trichomes) on the same organ are less clear.

The secretory cavity of glandular trichomes on different plants is reported to be bounded by a cuticle that becomes distended during its development (Tschirch and Stock, 1933; Amelunxen, 1965; Fridvalszky, Rakovan, and Keresztes, 1970; De Pasquale, 1974; Dayanandan and Kaufman, 1976; Peterson and Vermeer, 1984; Thomson and Healey, 1984). Our studies of the dermal sheath of the secretory cavity in *Cannabis* L. show it to consist not only of cuticle, but also a subcuticular cellulosic wall that grows during development and distension of this cavity (Hammond and Mahlberg, 1977, 1978; Kim and Mahlberg, 1991).

There is a consensus that precursors for cuticular components, including waxes, are synthesized in the dermal cells (Kolattukudy, 1980). However, considerable controversy surrounds the secretory mechanism for transport of these substances from the cell through the wall and cuticle during development. It has been proposed that waxes, for example, are exuded to the outer cuticular surface: through pores (Hall, 1967), through lamellate regions in the cuticle (Hallam, 1982), in a volatile fluid (Baker, 1982), or by molecular diffusion (Jeffree, Baker, and Holloway, 1975).

Development of the secretory cavity in *Cannabis* is associated with growth of a subcuticular wall formed from precursors derived from a nonlipoidal compartment in the secretory cavity (Kim and Mahlberg, 1991). Other components in the secretory cavity include an abundance of membraned secretory vesicles originating at the disc cell wall surface and deposited into the secretory cavity. Concomitant with growth of the subcuticular wall is the development of a prominent cuticle as part of the dermal sheath of the secretory cavity. Little is known about the structure of this cu-

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ticle; thus a study of its development can provide new information on cuticle formation in plants.

In this study we examine the development of the cuticle during formation of the glandular trichome and its secretory cavity. Our objectives include determination of 1) the distribution of the cuticle on the gland and adjacent dermal surfaces during early development of the trichome, 2) the deposition and growth of cuticle during secretory cavity enlargement, and 3) the source of precursors for cuticle growth over the secretory cavity. A unique feature in the development of the noncellular secretory cavity is cuticle growth in the absence of its direct contact with the disc cells which, like other dermal cells, are assumed to be the source of precursors for cuticle development.

MATERIALS AND METHODS

Procedures employed in this study of glandular trichomes on the bracts of pistillate plants of *Cannabis* are the same as those described previously (Kim and Mahlberg, 1991).

Cuticle measurements were derived from glandular trichomes grouped into progressive stages of development: presecretory (stages 1–3), early secretory (stages 4–7), and secretory (stages 8–13) phases. Measurements of trichome and dermal cell cuticles for a given stage were obtained from the same micrograph. For several stages only trichome cuticles were measured because dermal cells were not on the micrograph. Each datum point on the graph represents the average of three measurements. Standard deviation is represented by the vertical bar.

RESULTS

The general development of glandular trichomes on *Cannabis* has been described (Hammond and Mahlberg, 1977, 1978; Kim and Mahlberg, 1991).

Both the glandular trichome initial and the protoderm cells of the young bract possessed a comparably thin cuticle (Fig. 1). It was evident as a thin electron-dense zone covering a thickened cell wall. A thin layer of material interpreted to be wax was present over the cuticular surface. The thin cuticle persisted on the protoderm and developing gland initial as the latter formed the discoid layer of secretory cells, the subtending stipe cell, and the basal cell embedded in the dermal layer of the bract (Fig. 2).

The cuticular layer remained thin on the wall of the disc cells during their division to form the tier of disc cells as well as during their initial period of enlargement (Fig. 3). The cuticle on adjacent protoderm cells also remained thin on these cells during the early development of the bract.

A pattern of differential cuticle thickening on the trichome, as contrasted to the adjacent dermal cells, became evident during differentiation of the disc cells (Fig. 4). A thickened cuticle appeared over the entire outer wall surface of the disc cells and extended a short distance onto the wall of the stipe cell. A thickened cuticle did not cover the entire surface of the stipe cell, nor did it extend to the walls of the basal or dermal cells.

Cuticle thickening continued on the outer wall of the disc cells during their further enlargement phase preceding formation of the secretory cavity (Fig. 5). The increase in thickness of cuticle was evident upon comparing its thickness on walls of disc cells at different stages in development (Figs. 4, 5). The cuticle was thinner on the stipe cell wall than on the wall of the disc cells, and was very thin on the wall at the juncture of stipe and basal cells. The cuticle on the disc wall appeared to be deposited as a layer. At the juncture of the disc and stipe cells the thickened cuticle did not appear to be in direct contact with the electron-dense wall; rather, it bridged the acute angle formed by the walls of these adjoining cells. The intervening zone between the cuticle and wall

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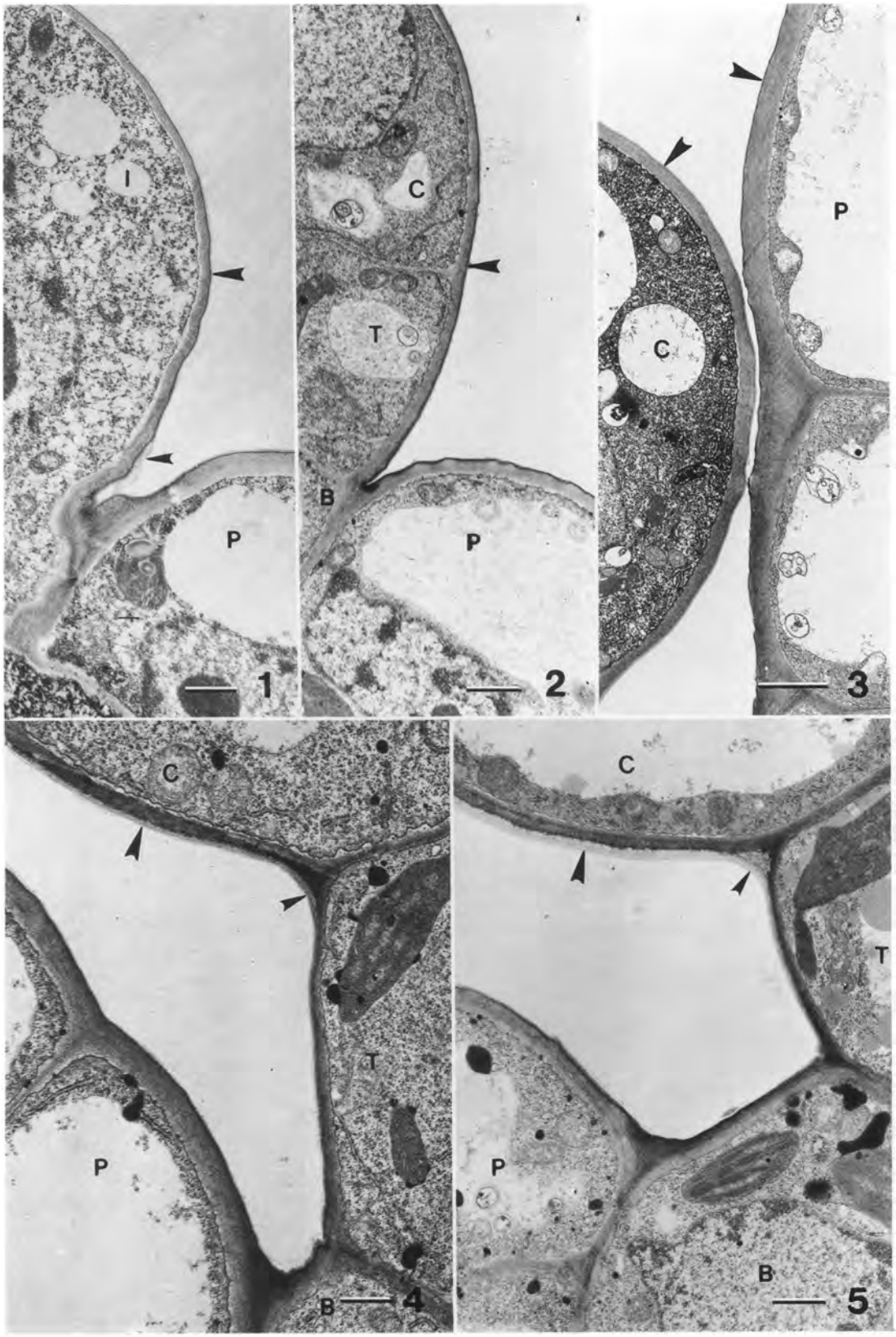
Figs. 1–5. Glandular trichome development shown in longisectional view. **1.** Trichome initial (I) showing a thin electron-dense cuticle (large arrowhead) that extends over protoderm (P). A thin wax layer (small arrowhead) is evident. Bar = 1 μm. **2.** A thin cuticle (arrowhead) is present over the trichome, now consisting of a two-celled discoid tier (C), stipe (T), and basal (B) cells, as well as over the dermal cell (P). Bar = 1 μm. **3.** Only a thin cuticle (arrowheads) is evident on walls of the dermal (P) and disc cell (C) even after development of a multicelled tier of disc cells. Bar = 1 μm. **4.** A thickening of cuticle (large arrowhead) becomes evident on outer wall of disc cells (C), but is not evident on dermal cells (P). Thickened cuticle bridges the juncture angle (small arrowhead) between disc and stipe (T) cells. Bar = 1 μm. **5.** Thickening of cuticle (large arrowhead) continues on wall of disc cells (C) as they enlarge, but before formation of the secretory cavity. Cuticle thickening also is evident at the juncture angle (small arrowhead) between disc (C) and stipe (T) cells although it does not cover entire stipe wall surface. No similar cuticle thickening is evident on walls of basal (B) or dermal (P) cells. Bar = 1 μm.



contained dense material but it was unlike that of either wall or cuticle (Figs. 4, 5).

A thickened cuticle was evident on the disc cell wall upon formation of the secretory cavity (Fig. 6). Development of this cavity from the disc cell wall was associated with the appearance of a dermal sheath consisting of the cuticle and a subcuticular wall (Kim and Mahlberg, 1991), both of which grew to form a much distended secretory cavity in the mature trichome.

Cuticle thickening of the disc cell wall was controlled individually by each trichome. Thus, trichomes at different stages in development possessed cuticles of different thicknesses. Since new trichomes were initiated among existing trichomes (Turner, Hemphill, and Mahlberg, 1980), disc cells of glands with thickened cuticle were present adjacent to glands with thin cuticle (Fig. 7). Similarly, the dermal cell, adjacent to the less developed trichome in this same micrograph, possessed a thin cuticle comparable to that of the adjacent trichome (Fig. 8).

An unusual phenomenon associated with trichomes in contact with each other was the fusion of thickened cuticles between two glands (Fig. 9). Fusion of cuticle occurred along the entire 1-μm length of contact of these surfaces in the depicted figure. A layer interpreted to be wax was present on the cuticular surfaces of both glands adjacent to the fused surfaces. Observations of contact areas of other contiguous cuticular surfaces indicated that these presumed wax layers also could fuse (Figs. 7, 8).

Cuticle over the disc cells continued to thicken during the formation of the secretory cavity and the accumulation of secretory vesicles in the cavity (Fig. 10). These vesicles became conspicuous components between the disc cell wall and the subcuticular wall of the secretory cavity. Each vesicle was bounded by a membrane (Fig. 10, insert). The vesicles appeared to be the source of precursors for cuticle development. Vesicles of different sizes, but similar electron density, were present throughout the cavity and some impinged upon the subcuticular wall of the dermal sheath. Vesicles of discernibly different appearance and an electron-light content also were present in the secretory cavity and were observed adjacent to the subcuticular wall (Figs. 11, 12).

The vesicles were densely aggregated in the secretory cavity, particularly during later stages in gland development (Fig. 10). During early stages in the secretory cavity these vesicles appeared less densely packed, but they often contacted each other in a loose array in the electron-light compartment (Fig. 12). Electron-dense material was evident in the secretory cavity surrounding the secretory vesicles (Figs. 11, 12). Electron-dense particles, approximately 0.04 μm diam, were associated with the outer surface of the vesicles as well as with material in the secretory cavity (Fig. 12).

Secretory vesicles, upon contacting the subcuticular wall, fused with it (Fig. 13). Their contents appeared to penetrate into the loosely structured components of this wall. Penetration into the wall was facilitated by the dissolution of the vesicular membrane. Whereas the membrane of the vesicles was evident at a position distant from the wall, it was not evident on that portion of the vesicle where it impinged upon the wall (Fig. 14).

Following dissolution of the vesicular membrane the contents of the vesicle moved through the wall to the subcuticular wall-cuticle interface. Electron-light zones in the wall, somewhat smaller in size than adjacent vesicles in the secretory cavity, were interpreted as the

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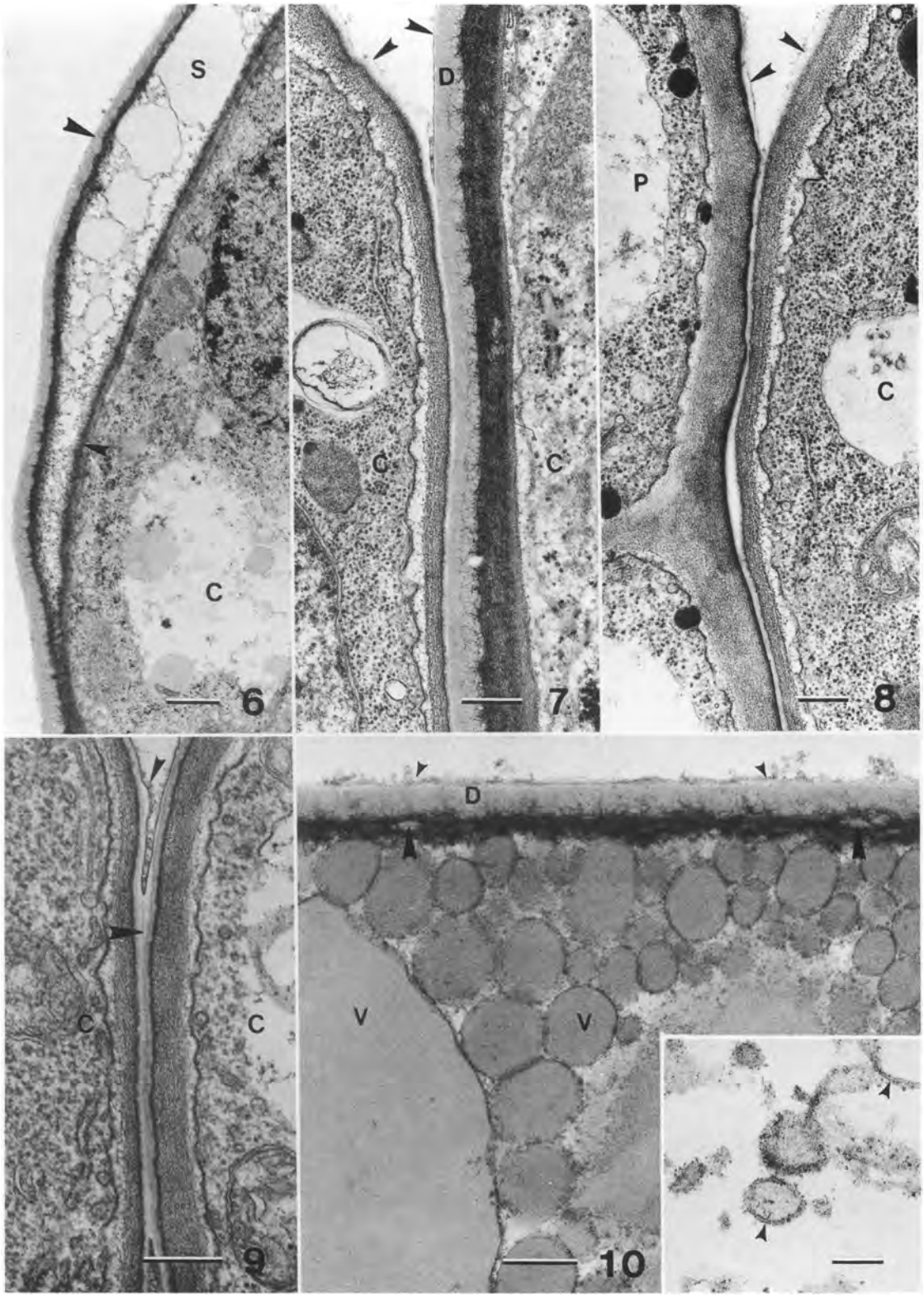
Figs. 6–10. Cuticle on outer wall of disc cells shown in sectional views. **6.** Thickening of cuticle (large arrowhead) is evident on the dermal sheath after formation of the secretory cavity (S) and on wall (small arrowhead) of disc cell (C) subjacent to the cavity (lower left). The disc cell wall separates along its midplane to form a subcuticular wall covered with cuticle (large arrowhead) while retaining a wall surface (small arrowhead) facing the secretory cavity. Bar = 0.5 μm. **7.** Cuticle thickening occurs independently on each gland. An enlarged gland (right) can possess a thickened cuticle whereas an immature gland (left) can possess a thin cuticle. Both glands are in contact with each other. Layers interpreted as wax (arrowheads), evident on both cuticular surfaces, appear to be fused where cuticle surfaces contact each other (below arrowheads). C, disk cell; D, cuticle. Bar = 0.25 μm. **8.** Differences in cuticle and wall thickness are evident between the disc cell of an immature gland (C) possessing a thin cuticle on the thin wall, and the dermal cell (P) possessing a thickened wall with an electron-dense layer of a thin cuticle. Layers intepreted as wax (arrowheads) appear fused where their surfaces contact each other (below arrows). Bar = 0.25 μm. **9.** Fused cuticles (large arrowhead) between two disc cells (C) of contiguous glands. Wax is represented by a granular material (small arrowhead) on cuticle surfaces adjacent to a fused cuticle surface approximately 1 μm long. Bar = 0.25 μm. **10.** Secretory vesicles (V) of different sizes are evident in the secretory cavity. Cuticle (D) is subtended by a subcuticular wall containing electron-light zones (arrowheads) interpreted to represent vesicular contents being transported from the secretory cavity to the cuticle. Material interpreted as wax covers the cuticle (small arrowheads). Vesicles (arrowheads) possess a membrane (insert). Bar = 0.5 μm. Bar in insert = 0.1 μm.



contents of vesicles in transit through the subcuticular wall to the cuticle (Fig. 10). The irregular masses of cuticle at the subcuticular wall-cuticle interface represented quantities of secretory material derived from these vesicles (Fig. 14). This deposition of cuticular precursors from the vesicles resulted in thickening of the cuticle along its entire inner surface. Their solidification appeared to occur rapidly and close to the site of precursor release from the secretory vesicles.

Deposition of new cuticular materials at its surface facing the secretory cavity occurred in the presence of wall material that surrounded the vesicles of precursors as they were transported through the wall to the wall-cuticle interface. As a result, residual quantities of this wall material became interspersed in the cuticle as new deposits of cuticular material were laid down at different positions along this interface. The precursors were deposited as irregular masses of new cuticle. The cuticle deposits were separated by dark strands of wall material, which imparted a dendroid or reticulated appearance to recently deposited cuticle (Figs. 14, 15).

These dark strands of wall material were present throughout the cuticle and radiated in various directions (Figs. 13, 14). The area of wall material was widest at the subcuticular wall-cuticle interface, the site of new cuticle deposition. The narrow regions were deep within the cuticle, toward the outer surface of the sheath where deposition of cuticle over a period of time appeared to form a more dense cuticular layer. These strands of wall material were never observed to extend to the outer surface of the cuticle (Figs. 14, 15). The dendroid projections of wall material in the cuticle appeared to decrease as additional quantities of cuticular materials thickened the cuticle by filling in the branchlike extensions of wall materials (Fig. 16).

A thin layer of material on the outer surface of the dermal sheath of the secretory cavity was interpreted to be wax (Figs. 15, 16). This layer was more conspicuous on the sheath of glands with enlarged secretory cavities than on those with secretory cavities at earlier stages in development.

The cuticle of the glandular trichome and particularly of the dermal sheath of the secretory cavity underwent growth in thickness during development of the gland (Fig. 17). The cuticle of the trichome initial (A) and bracteal dermal cells (B) were similar in thickness (stages 1–3). Cuticle of the sheath increased in thickness during the early phases in development of the secretory cavity (stages 4–7). The cuticle increased markedly in thickness during later stages in enlargement and distension of the secretory cavity (stages 8–13). The cuticle of the sheath increased nearly eightfold in thickness, from 38 to 303 nm, during enlargement of the secretory cavity. The cuticle of dermal cells of the bract showed little increase in thickness compared to that on the trichome.

DISCUSSION

Cuticle formation on the sheath of glands of *Cannabis* was observed to be controlled by the trichome. Since new gland initials are formed throughout bract and leaf ontogeny (Turner, Hemphill, and Mahlberg, 1980), the mechanism controlling cuticle deposition must reside in the trichome, and must be independent of cuticle deposition in dermal cells. Cuticle

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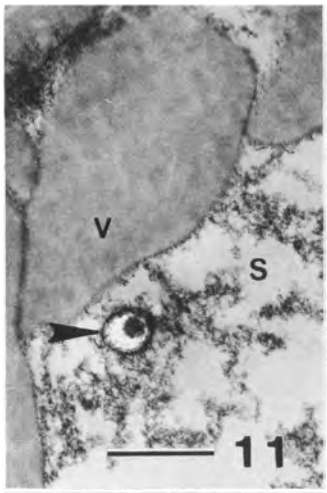
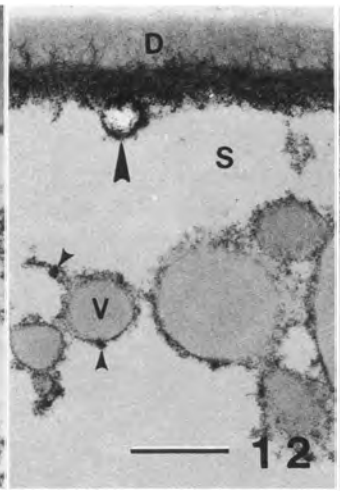
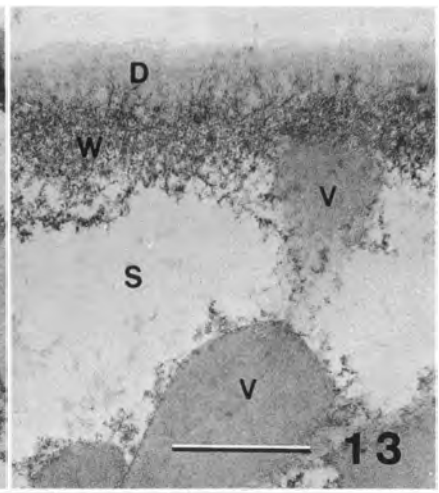
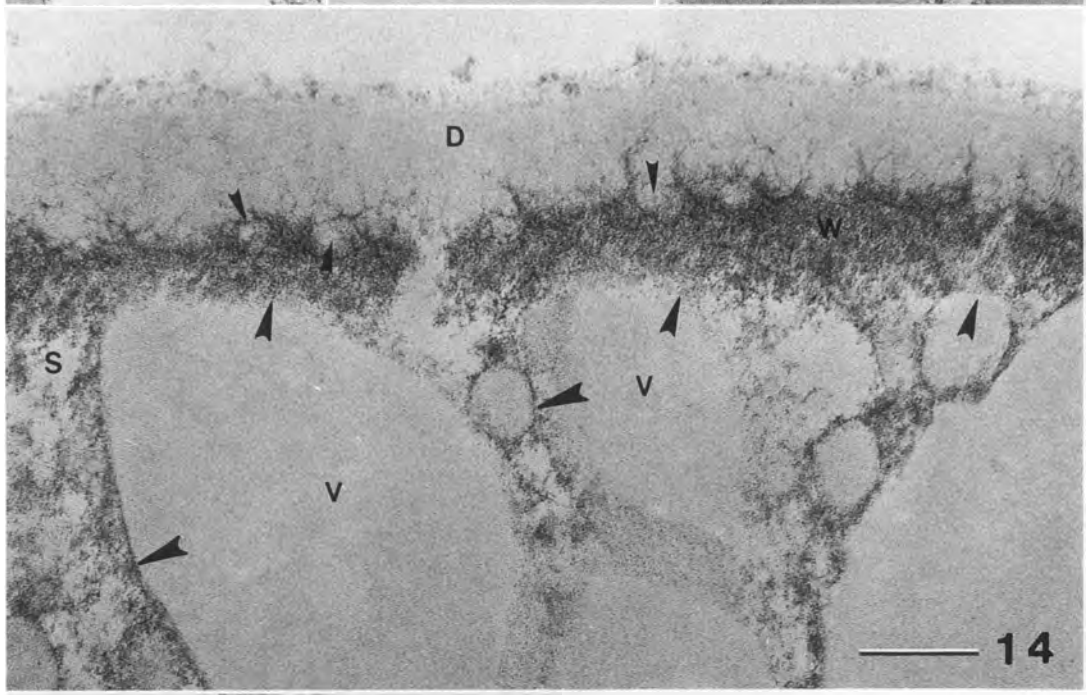
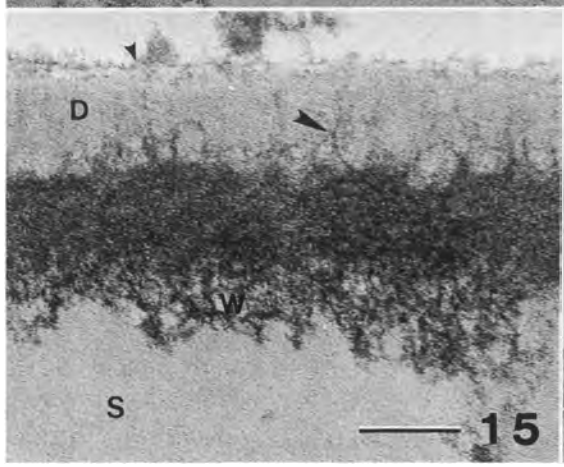
Figs. 11–16. Secretory cavity and its contents shown in longisectional view. **11.** Secretory cavity (S) showing vesicles of different composition. A vesicle with an electron-light content and including small dense body (arrowhead) contrasts with vesicles (V) containing a more uniform electron-dense content. Bar = 0.25 μm. **12.** Electron-light vesicle (large arrowhead) adjacent to wall of dermal sheath differs in electron density, and possibly in composition, from other electron-dense vesicles (V) in secretory cavity (S). Small arrowheads, electron-dense particles. D, cuticle. Bar = 0.25 μm. **13.** Vesicle (upper V) appears to fuse with loosely aggregated subcuticular wall (W). Wall materials extend into the cuticle (D). S, secretory cavity. Bar = 0.25 μm. **14.** Membranes (large arrowheads) of secretory vesicles (V) appear to disorganize where they contact (medium arrowhead) the subcuticular wall (W) below the cuticle (D). New cuticle is deposited at the subcuticular wall-cuticle interface (small arrowheads) resulting in an irregular or knobby inner cuticle surface. Fine extensions of wall material, which nearly encompass recently deposited cuticle, are evident deep in the cuticle in relation to previously deposited quantities of cuticle. Bar = 0.2 μm. **15.** Dermal sheath showing electron-dense wall materials (large arrowhead) permeating cuticle (D) during thickening process giving rise to a dendroid pattern in cuticle. This pattern is evident along entire inner surface of cuticle during thickening process. Wall extensions visible near the outer surface of cuticle represent residues of wall that surrounded cuticular precursors deposited during early phases of cuticle thickening. A layer interpreted as wax (small arrowhead) is present on surface of the cuticle. S, secretory cavity. Bar = 0.1 μm. **16.** Thickened dermal sheath of secretory cavity showing residual wall material (large arrowhead) of subcuticular wall (W) extending deep into cuticle (D). These wall extensions do not represent special pores in cuticle although they could be sites of weakness in the dermal sheath. The cuticle appears to become compacted or more dense during development, making the dendroid pattern less evident in the cuticle. A layer interpreted as wax (small arrowhead) is evident on surface of the cuticle. S, secretory cavity. V, secretory vesicle. Bar = 0.1 μm.

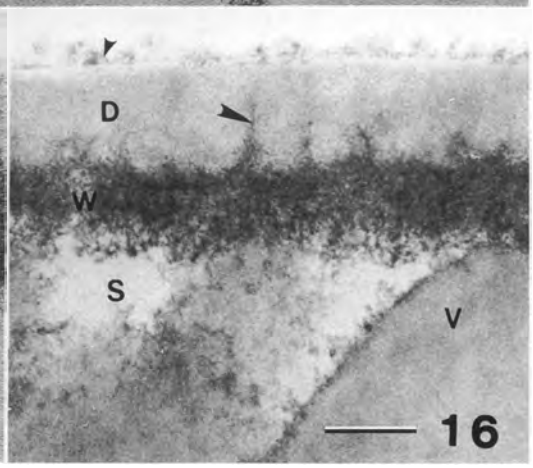












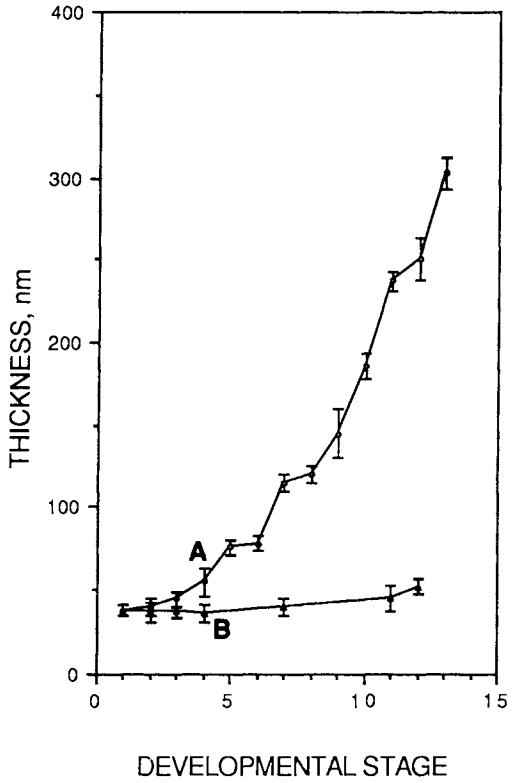


Fig. 17. Cuticle thickness of sheath and dermal cells during glandular trichome development. Cuticle thickness on sheath (A) was simlar to that of dermal cells (B) during early development of trichome (stages 1–3). Upon formation of the secretory cavity, and enlargement in diameter during growth of the gland, the sheath cuticle increased nearly eightfold in thickness (stages 4–13). Cuticle of bracteal dermal cells (B) showed little change in thickness compared to that of trichomes of different developmental stages.

thickening occurred over the entire spherical surface of the sheath which also expands fourfold in surface area for each doubling in diameter of the gland. It is unclear what phenomenon triggered and controlled this thickening process on the surface of the disc cell, because the thickening process was detected before formation of the noncellular secretory cavity (Kim and Mahlberg, 1991).

Precursors for cuticle development of the disc cell wall and dermal sheath were derived from the membraned secretory vesicles in the noncellular secretory cavity. The observed thickening of cuticle at the subcuticular wall-cuticle interface in the sheath distant from the disc cells suggests that these cells somehow transferred the information to control the thickening process across the noncellular secretory cavity and distant from these cells to the site of cuticle deposition. Vesicles of different morphologies and physical characteristics in the cavity indicate that they may differ in composition and, upon dissolution of their membrane, contribute different components to the developing cuticle. Since these vesicles originate from the disc cells followed by their subsequent deposition into the secretory cavity (Kim and Mahlberg, 1991), it is possible that the disc cells impart differences both to membrane composition and vesicular contents in the developing vesicles. Although the fate of the membrane components is unknown, we speculate that they somehow contribute to the synthesis of the cuticle on the sheath.

The density and round shape of the secretory vesicles indicated that they represent lipophilic material dispersed in the hydrophilic contents of the secretory cavity. Whereas vesicles were abundant and closely packed in the secretory cavity of enlarged glands, fewer were evident in the cavity during initial stages of gland development. Flocculent material, possibly including wall matrix, was evident in the hydrophilic compartment. Electron-dense particles often were associated with the membrane of vesicles and other components in the secretory cavity. These particles were interpreted to represent those detected in the wall during the initial splitting of the wall to form the secretory cavity (Kim and Mahlberg, 1991). The composition and function of these particles is unknown.

Our observations suggest that cuticle development in the gland involves two phases: 1) a structural phase in which precursors solidify rapidly as deposits to thicken the cuticle, and 2) an amorphous phase in which precursors permeated the cuticle to its exterior surface to increase its girth or surface area during enlargement of the secretory cavity. Deposition of new cuticle was evident at the subcuticular wall-cuticle interface. The wall matrix, which partially surrounded the new deposits, imparted a dendritic appearance to the cuticle, similar to one of several types observed for cuticle in epidermal cells and described as channels for transport of waxes or other cuticular components (Hall, 1967; Lyshede, 1978; Holloway, 1982; Miller, 1985). Rather than channels, these dendritic processes represent areas of the wall matrix that surround cuticular deposits during the deposition process. This rapidly solidified deposition of cuticular precursors represents the structural phase, and involves the wall matrix in cuticle deposition.

Cuticle and wax fusion between contiguous glands supports an interpretation that there also exists an amorphous phase in cuticle deposition in which precursors permeate the structural phase in a liquified state, prior to their

solidification. The fusion of cuticles of contiguous glands is indicative that the precursors permeate to the cuticle surface of each gland and oxidize into a common cuticular layer to join these glands. The amorphous phase may contribute to the surface growth of the sheath in that precursors permeating structural cuticle in a liquid state facilitate the fourfold expansion of the surface area of the sheath during the extension growth, and only subsequently do they contribute to the structural phase upon their solidification.

Deposition of the structural phase for cuticle is documented morphologically in this study. The occurrence of an amorphous phase for cuticle is correlated with reports for wax formation in which precursors are interpreted to move through cuticle in a volatile state and oxidize on the cell surface as wax deposits (Baker, 1982). Permeation of the structured phase of cuticle with a liquid phase of cuticular components, as well as waxes, not only facilitates interpretation of the fusion phenomenon but also explains the progressive compaction of cuticle with the concomitant decrease in the dendroid extensions of wall material in the thickening cuticle.

Cuticular thickening may represent a derived response of trichomes in association with their secretory activity. Volatile monoterpenes contained in glands (Croteau and Johnson, 1984) are detected in *Cannabis* glands (Hammond, Kim, and Mahlberg, unpublished data) and can be detected as volatiles from plant material (Hood, Dames, and Barry, 1973). The secretory cavity containing secretory vesicles, as in *Cannabis,* is interpreted to represent a derived structural feature for glandular trichomes selected for an enhanced capacity to accumulate large quantities of volatile compounds and to transport them to the cuticular surface for vaporization from the gland surface. The cells that synthesize these volatile compounds simultaneously secrete other lipophilic compounds, for cuticle synthesis (Kolattukudy, 1980), possibly in the same vesicles, to provide structural strength to the growing cuticle of the gland.

Glandular trichomes such as those in *Cannabis* can serve as a working model to study morphogenetic and secretory processes in a specialized cell type, such as the disc cell. Techniques for isolating the secretory cavity contents (Lanyon, Turner, and Mahlberg, 1981), and analyses of the disc cells and composition of the sheath will provide a more complete understanding of cuticle development both on the glandular trichome and on the surface of dermal cells in general.

LITERATURE CITED

AMELUNXEN, F. 1965. Elektronenmikroskopische Untersuchungen an den Drüsenschuppen von *Mentha piperita* L. *Planta Medica* 13: 457–473.

BAKER, E. A. 1982. Chemistry and morphology of plant epicuticular waxes. *In* D. F. Cutler, K. L. Alvin, and C. E. Price [eds.], The plant cuticle, 139–166. Academic Press, London.

CROTEAU, R., AND M. A. JOHNSON. 1984. Biosynthesis of terpenoids in glandular trichomes. *In* E. Rodriguez, P. L. Healey, and I. Mehta [eds.], Biology and chemistry of plant trichomes, 133–184. Plenum Press, New York.

CUTLER, D. F., K. L. ALVIN, AND C. E. PRICE. 1982. The plant cuticle. Academic Press, London.

DAYANANDAN, P., AND P. B. KAUFMAN. 1976. Trichomes of *Cannabis sativa* L. (Cannabaceae). *American Journal of Botany* 63: 578–591.

DE PASQUALE, A. 1974. Ultrastructure of the *Cannabis sativa* glands. *Planta Medica* 25: 238–248.

FRIDVALSZKY, L., J. RAKOVAN, AND A. KERESZTES. 1970. Development of the glandular cell in the epidermis of *Silene armeria. In* P. Favard [ed.], International conference on electron microscopy 7, vol. 3, 427–428. Société Francaise de Microscopie Electronique, Paris.

HALL, D. M. 1967. The microchannels in the epidermis of white clover. *Science* 158: 505–506.

HALLAM, N. D. 1982. Fine structure of the leaf cuticle and the origin of leaf waxes. *In* D. F. Cutler, K. L. Alvin, and C. E. Price [eds.], The plant cuticle, 197–214. Academic Press, London.

HAMMOND, C. T., AND P. G. MAHLBERG. 1977. Morphogenesis of capitate glandular hairs of *Cannabis sativa* (Cannabaceae). *American Journal of Botany* 64: 1023–1031.

———, AND ———. 1978. Ultrastructural development of capitate glandular hairs of *Cannabis sativa* L. (Cannabaceae). *American Journal of Botany* 65: 140–151.

HOLLOWAY, P. J. 1982. Structure and histochemistry of plant cuticular membranes: an overview. *In* D. F. Cutler, K. L. Alvin, and C. E. Price [eds.], The plant cuticle, 1–32. Academic Press, London.

HOOD, L. V. S., M. E. DAMES, AND G. T. BARRY. 1973. Headspace volatiles of marijuana. *Nature* 242: 402–403.

JEFFREE, C. E., E. A. BAKER, AND P. J. HOLLOWAY. 1975. Ultrastructure and recrystallization of plant epicuticular waxes. *New Phytologist* 75: 539–549.

JUNIPER, B., AND R. SOUTHWOOD. 1986. Insects and the plant surface. Edward Arnold, London.

KIM, E. S., AND P. G. MAHLBERG. 1991. Secretory cavity development in glandular trichomes of *Cannabis sativa* L. (Cannabaceae). *American Journal of Botany* 78: 142–151.

KOLATTUKUDY, P. E. 1980. Biopolyester membranes in plants: cutin and suberin. *Science* 208: 990–1000.

LANYON, V. S., J. C. TURNER, AND P. G. MAHLBERG. 1981. Quantitative analysis of cannabinoids in the secretory product from capitate-stalked glands of *Cannabis sativa* L. (Cannabaceae). *Botanical Gazette* 142: 316–319.

LYSHEDE, O. B. 1978. Studies on outer epidermal cell walls with microchannels in a xerophytic species. *New Phytologist* 80: 421–426.

MARTIN, J. T., AND B. E. JUNIPER. 1970. The cuticles of plants. Edward Arnold, Edinburgh.

MILLER, R. H. 1985. The prevalence of pores and canals

in leaf cuticular membranes. *Annals of Botany* 55: 459–471.

PETERSON, R. L., AND J. VERMEER. 1984. Histochemistry of trichomes. *In* E. Rodriguez, P. L. Healey, and I. Mehta [eds.], Biology and chemistry of plant trichomes, 71–94. Plenum Press, New York.

THOMSON, W. W., AND P. L. HEALEY. 1984. Cellular basis of trichome secretion. *In* E. Rodriguez, P. L. Healey, and I. Mehta [eds.], Biology and chemistry of plant trichomes, 95–111. Plenum Press, New York.

TSCHIRCH, A., AND E. STOCK. 1933. Die Harze, vol. 1. Gebrüder Borntraeger, Berlin.

TURNER, J. C., J. K. HEMPHILL, AND P. G. MAHLBERG. 1980. Trichomes and cannabinoid content of developing leaves and bracts of *Cannabis sativa* L. (Cannabaceae). *American Journal of Botany* 67: 1397–1406.