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SECRETORY CAVITY DEVELOPMENT IN GLANDULAR TRICHOMES OF CANNABIS SATIVA L. (CANNABACEAE)[1]

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Development of the secretory cavity and formation of the subcuticular wall of glandular trichomes in *Cannabis sativa* L. was examined by transmission electron microscopy. The secretory cavity originated at the wall-cuticle interface in the peripheral wall of the discoid secretory cells. During the presecretory phase in development of the glandular trichome, the peripheral wall of the disc cells became laminated into a dense inner zone adjacent to the plasma membrane and a less dense outer zone subjacent to the cuticle. Loosening of wall matrix in the outer zone initiated a secretory cavity among fibrous wall materials. Membrane-bound hyaline areas, compressed in shape, arose in the wall matrix. They appeared first in the outer and subsequently in the inner zone of the wall. The membrane of the vesicles, and associated dense particles attached to the membrane, arose from the wall matrix. Hyaline areas, often with a conspicuous electron-dense content, were released into the secretory cavity where they formed rounded secretory vesicles. Fibrous wall material released from the surface of the disc cells became distributed throughout the secretory cavity among the numerous secretory vesicles. This wall material was incorporated into the developing subcuticular wall that increased five-fold in thickness during enlargement of the secretory cavity. The presence of a subcuticular wall in the cavity of *Cannabis* trichomes, as contrasted to the absence of this wall in described trichomes of other plants, supports a polyphyletic interpretation of the evolution of the secretory cavity in glandular trichomes among angiosperms.

The secretory cavity of a capitate glandular trichome in *Cannabis* represents a large depository formed above a group of specialized secretory cells. This cavity is a noncellular feature formed in association with the cell wall and cuticle of the secretory cells. The bounding dermal sheath of the secretory cavity is typically described as a cuticular layer for glandular trichomes of *Cannabis* as well as other plants (Amelumxen, 1965; Fridvalszky, Rakovan, and Keresztes, 1970). Recent studies, however, have demonstrated the presence of a subcuticular cellulosic wall bounding the dermal sheath of this trichome in *Cannabis* (Hammond and Mahlberg, 1978; Mahlberg et al., 1984). As yet, the origin and development of the subcuticular wall, and secretory cavity, is not well understood.

Enlargement of the glandular trichome is associated with deposition of secretions into the secretory cavity by secretory cells. During glandular trichome development the dermal sheath increases several-fold in surface area, a process requiring the availability of wall substrates in the secretory cavity for formation of the new wall under the cuticle. Although the origin of these substrates must be related to the secretory cells, little is known concerning processes associated with development of the subcuticular wall.

In this study we examine the development of the secretory cavity and its dermal sheath. Our objectives include determination of the 1) origin and early development of the secretory cavity, 2) pattern of compartmentalization of components in the secretory cavity, and 3) origin of the subcuticular cell wall. As an outcome of this investigation we also describe the unusual extracellular processes of simultaneous degradation of cell wall from secretory cells and organization of new wall associated with development of the dermal sheath.

MATERIALS AND METHODS

Various developmental stages of bracts, containing glandular trichomes, were collected from plants of *Cannabis sativa* L., grown under greenhouse conditions (Hammond and Mahlberg, 1973). The bracts were cut into small pieces and fixed in a solution containing 6.6% glutaraldehyde, 3% dimethyl sulfoxide (DMSO), in sodium cacodylate buffer (pH 7.2)

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for 70 hr at 4 C. After fixation the tissues were washed in 50 mM cacodylate buffer and postfixed with aqueous 2% osmium tetroxide vapor for 2.5 hr at room temperature. This glutaraldehyde concentration in DMSO for a prolonged cold fixation period aided penetration of the fixative to yield a good fixation image for glandular trichomes. Vapor osmication was employed to control postfixation to a gray-black color and minimize overreaction. Tissue pieces were immersed in buffer in one well of a spot plate along with a drop of osmium tetroxide in an adjacent well. The spot plate was maintained in a covered petri dish in the hood for the fixation period. Tissues were rinsed several times in deionized water to remove buffer, dehydrated in a graded ethanol-acetone series, and embedded in Spurr's resin (1969). Thin sections were cut on a LKB-IV ultramicrotome with glass or diamond knives and stained with uranyl acetate followed by lead citrate (Reynolds, 1963). Sections were examined and photographed with a Philips EM 300 transmission electron microscope at 60 kV.

Wall measurements were derived from glandular trichomes grouped into progressive stages of development: the presecretory phase (stages 1–3) included the enlarged epidermal initial and early stages in formation of the discoid group of secretory cells; the early secretory phase (stages 4–7) included formation and initial enlargement of the secretory cavity; and the secretory phase (stages 8–13) included progressive distention of the dermal sheath and enlargement of the secretory cavity to form the mature trichome. Each datum point of the graph represents the average of three wall measurements.

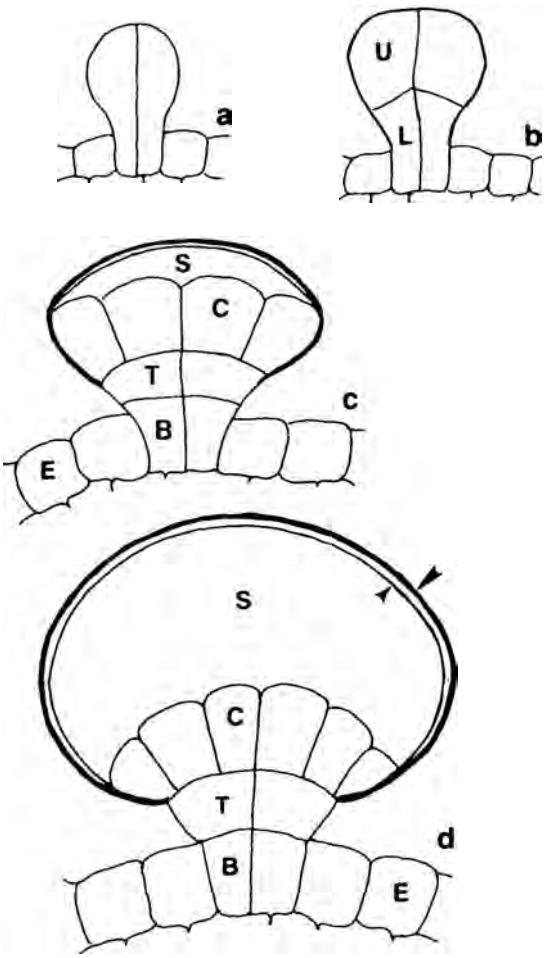


Fig. 1. Diagram depicting development of glandular trichome. a. Trichome initiation occurs upon enlargement of a protodermal cell that is bisected by an anticlinal division. b. A periclinal division separates an upper (U) from a lower (L) tier of cells. c. Anticlinal divisions in the upper tier form a discoid tier of secretory cells (C) from which a portion of the outer wall with cuticle separates to initiate formation of the secretory cavity (S). A periclinal division in lower tier forms the stipe (T) and basal cells (B) of gland. d. Mature glandular trichome possesses an enlarged secretory cavity (S) covered with cuticle (large arrowhead) and subjacent cell wall (small arrowhead) formed from the discoid tier of 8–13 secretory cells (C) subtended by a stipe (T) supported by a tier of basal cells (B) embedded in the epidermis (E).

RESULTS

Initiation of the glandular trichome occurred upon a vertical enlargement of a protodermal cell to form a gland initial that was subsequently bisected by an anticlinal division (Fig. 1). A periclinal division separated an upper pair of cells, that will form the secretory tier, from a lower auxiliary tier. The auxiliary tier typically divided periclinally to form a tier of stipe cells, which support the secretory tier, and a lower tier of basal cells embedded in the epidermis. The secretory cells underwent additional anticlinal divisions to form a tier of 8–13 secretory cells arranged in the form of a disc. A secretory cavity was formed above the discoid secretory cells upon separation of a cuticle-wall dermal sheath which enlarged to form the distended secretory cavity (Fig. 1a–d; Hammond and Mahlberg, 1978). Descriptively, cells of the discoid tier are referred to as disc cells to distinguish them from stipe and basal cells which also may have secretory activity.

The outer wall of disc cells prior to development of the secretory cavity was more or less uniform in density and possessed a thin cuticle over its surface (Fig. 2). However, a narrow electron-light zone was evident in the wall along the surface facing the plasma mem-

brane and extended along the anticlinal walls between adjacent cells. Just prior to initiation of the secretory cavity this wall became differentially dense. The inner zone adjacent to the plasma membrane became electron dense, whereas the outer zone of the wall, extending to the cuticle, became less dense in appearance (Fig. 3). Both wall zones when first detectable were approximately equal in thickness over the disc cells although the outer zone was conspicuously thicker at juncture regions between adjacent disc cells.

Secretory cavity formation—Secretory cavity formation was initiated upon loosening of wall material that became fibrous in appearance (Fig. 4). An enlarged clear region appeared in the wall, which we interpret to form the secretory cavity within the loosened wall matrix. Wall fibrils bridged this incipient secretory cavity in the outer wall zone. A thin layer of wall material persisted under the cuticle as the secretory cavity became evident in the wall. Upon continued loosening of wall components, several structural changes became evident in the wall. Small, somewhat dense bodies approximately 0.08 μm in diameter were evident in the incipient secretory cavity (Fig. 5). They appeared to be derived from the inner wall zone and became dispersed among particulate matter throughout the loosened wall matrix.

Concomitant with initial loosening of wall material in the outer wall zone was the development of enlarged and distinctive hyaline areas in this zone (Fig. 6). These hyaline areas, bounded by a membrane, were elongated in shape and of different sizes. In walls of some glandular trichomes they were very long, indicating that they may have fused in tandem to form much elongated areas. These areas also were evident in the more dense inner wall zone where they were smaller in size and more flattened in appearance in contrast to their form in the outer wall zone. Hyaline areas enlarged to form distinctive structures in the outer wall zone. Occasionally they possessed an electron-dense content of unknown character (Fig. 7). Dense bodies and particulate matter were evident in the wall matrix surrounding hyaline areas (Fig. 8). Hyaline areas continued to be formed and were present in both zones of the wall upon continued enlargement of the secretory cavity. Individual hyaline areas dissociated from the wall matrix and entered the secretory cavity where they appeared as flattened sacs. Particulate material remained associated with the membrane of these areas when in the secretory cavity, and dense bodies continued to be evident in the wall matrix. Other membrane-bound hyaline areas were evident in the outer wall zone near the periphery of the secretory cavity, whereas numerous and smaller hyaline areas were evident in the inner dense zone of the wall.

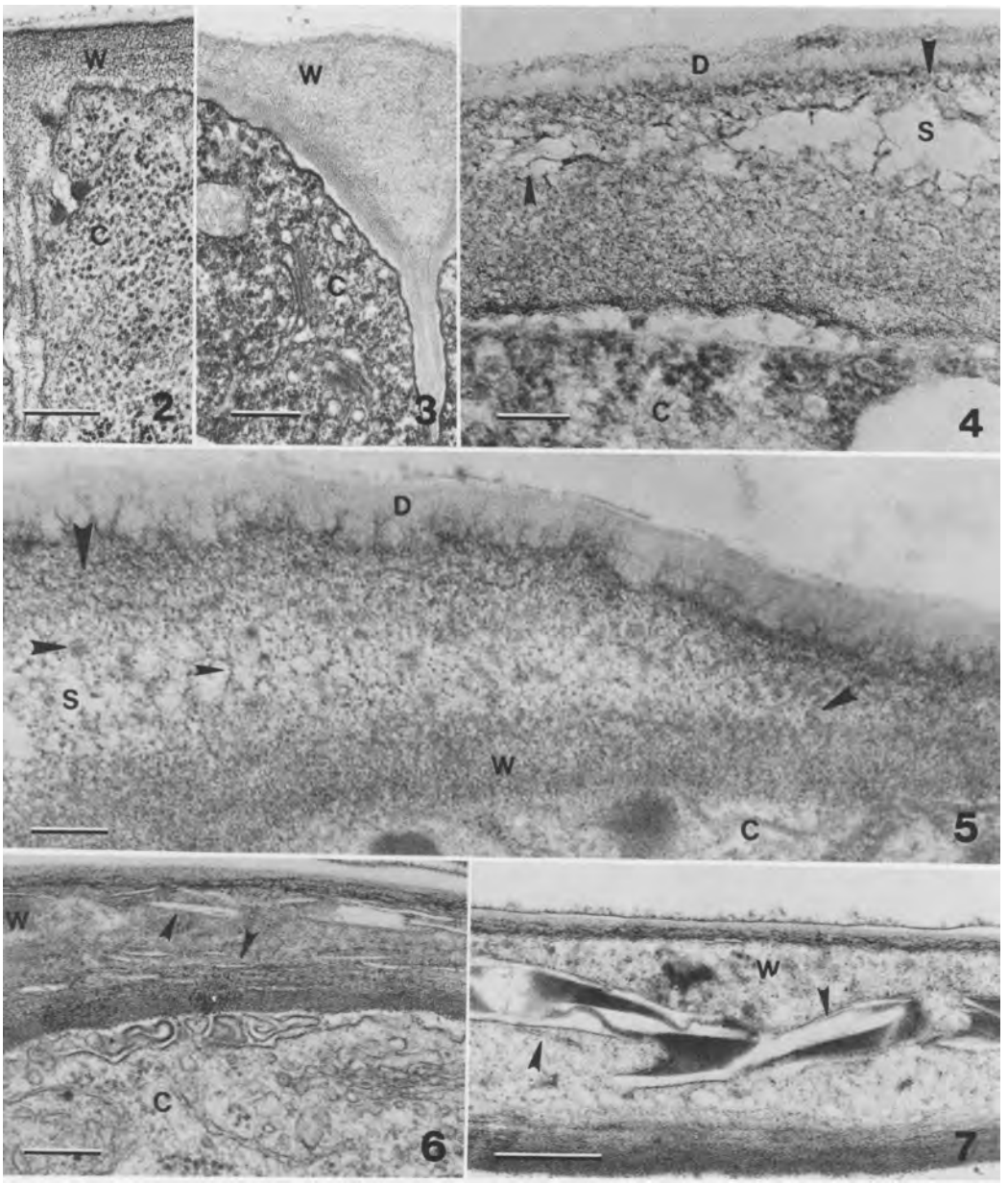
Additional hyaline areas were formed upon continued enlargement of the secretory cavity (Fig. 9). The entire disc cell wall surface facing the secretory cavity was active in producing these structures. Near the wall they appeared flattened or irregular in shape, whereas distant from the wall they were more or less round. The irregular shape and large size of some hyaline areas suggested that their enlargement resulted from fusion of several such structures. A hyaline area, now definable as a vesicle, when in the secretory cavity, was bounded by a unit membrane (Fig. 9, insert).

As the glandular trichome continued to enlarge, the secretory vesicles became large in size and closely packed in the secretory cavity (Fig. 10). Vesicles were evident throughout the secretory cavity including the juncture region where the wall of the disc cell joined the cuticle and subcuticular wall.

New hyaline areas continued to be formed from the disc cell wall as the secretory cavity enlarged (Fig. 11). As observed in earlier stages of secretory cavity development, they were flattened in appearance and their membrane appeared to be coated with particulate matter. When somewhat distant from the wall surface, these hyaline areas gave rise to the rounded vesicles. These vesicles were similar to those of large size and possessed a membrane that delimited an electron-dense content.

Subcuticular wall formation—The disc cell wall also was observed to perform a role in development of the subcuticular wall. The loosened character of the wall matrix of the outer zone of the disc cells was evident over their exposed wall surface facing the secretory cavity (Fig. 12). Quantities of material similar in character to wall matrix were widely distributed in the secretory cavity.

Wall material was released from the disc cell wall and accumulated in the secretory cavity (Fig. 13). This phenomenon appeared to occur along the entire wall surface where masses of wall matrix of different sizes were associated with the wall surface as well as distant from it. Hyaline areas also continued to be released from the wall along with wall matrix (Fig. 13). Other vesicles of different sizes, some irregular in shape, were present in the proximity of wall matrix in the secretory cavity. Also present were small and electron-dense particles; these



Figs. 2–7. Secretory cavity initiation. **2.** Electron-dense cell wall (W) of secretory cells (C) prior to secretory cavity development. Cuticle present on cell wall. Bar = 0.25 μm. **3.** Cell wall (W) of secretory cells (C) immediately prior to secretory cavity formation showing electron-light outer zone and more dense inner zone. Outer zone more prominent at cell junctures. Cuticle present on cell wall. Bar = 0.25 μm. **4.** Loosening of wall matrix (small arrowhead) in outer zone showing initial formation of secretory cavity (S) and presence of wall layer (large arrowhead) under cuticle (D). Fibrous wall material bridges incipient secretory cavity. C, secretory cell. Bar = 0.1 μm. **5.** Early formation of secretory cavity (S) showing loosened fibrous nature (small arrowhead) of outer wall zone. Dense bodies in secretory cavity (median arrowhead at left) originate from wall upon formation of secretory cavity (median arrowhead at right). Subcuticular wall is evident (large arrowhead) under cuticle (D). W, wall of disc cell; C, secretory cell. Bar = 0.1 μm. **6.** Disc cell wall (W) upon initiation of secretory cavity showing numerous hyaline areas of different sizes distributed in outer and inner zones of wall (arrowheads). Cuticle present on cell wall. C, secretory cell. Bar = 0.25 μm. **7.** Disc cell wall (W) showing several enlarged (large arrowhead) and small hyaline areas (small arrowhead) in outer wall zone. Cuticle present on cell wall. Bar = 0.25 μm.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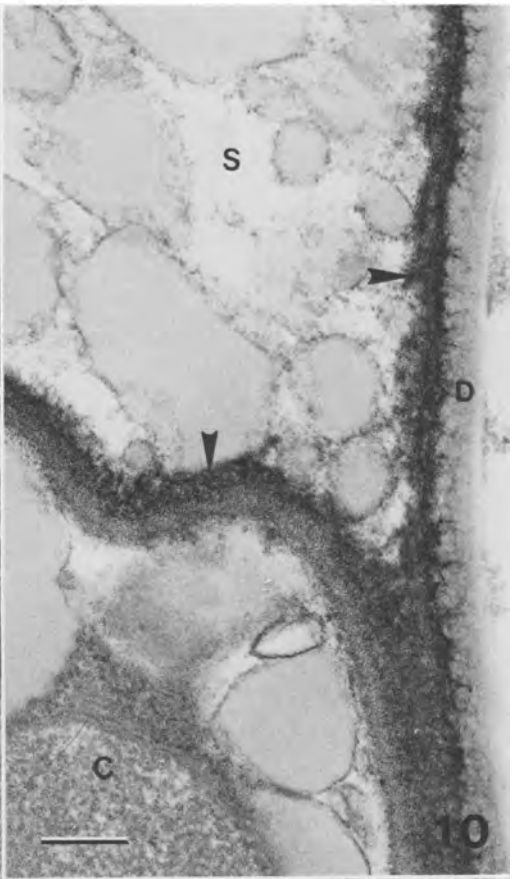
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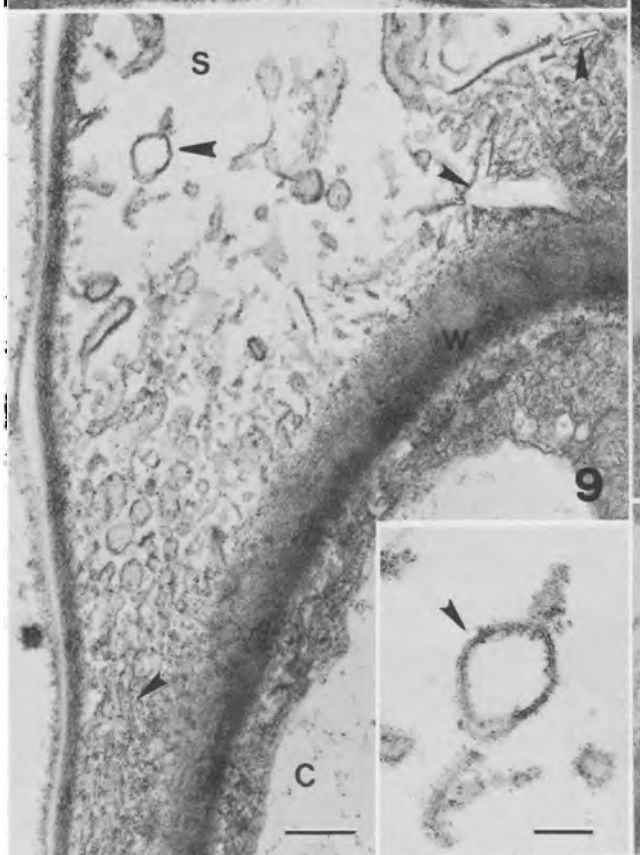
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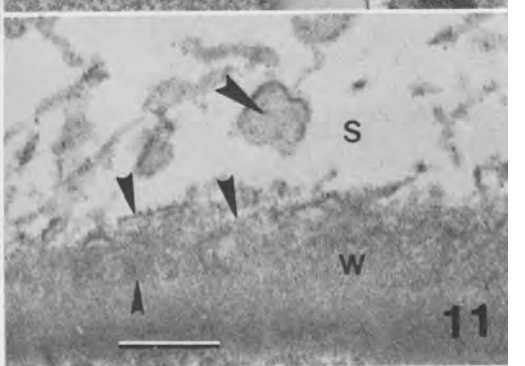
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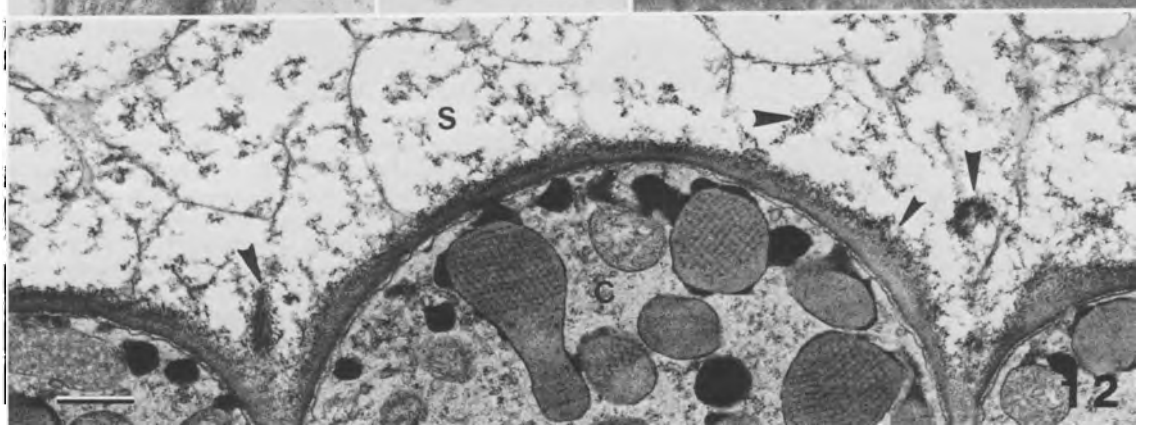
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were approximately the size of ribosomes evident in the cytoplasm of the disc cells. Origin of the dense particles in the secretory cavity was uncertain, although a few particles of similar density were evident in the cell wall.

Material comparable to wall matrix was evident throughout the secretory cavity among secretory vesicles (Fig. 14). Wall material was localized in the hydrophilic compartment between secretory vesicles. In glandular trichomes possessing an enlarged secretory cavity the secretory vesicles typically were more or less round in shape and relatively large in size when compared to vesicles in early phases of secretory cavity development. However, vesicles of small size were interspersed among those of large size.

The electron-dense subcuticular wall of the dermal sheath was continuous with the wall at the periphery of the secretory cavity where it joined with the wall of the disc cell (Fig. 9). Wall matrix in the secretory cavity was evident near the dermal sheath (Fig. 14). This wall matrix in the secretory cavity became associated with the dermal sheath and was incorporated into the subcuticular wall. This process appeared to include deposition of wall aggregates into the existing wall under the cuticle (Fig. 15).

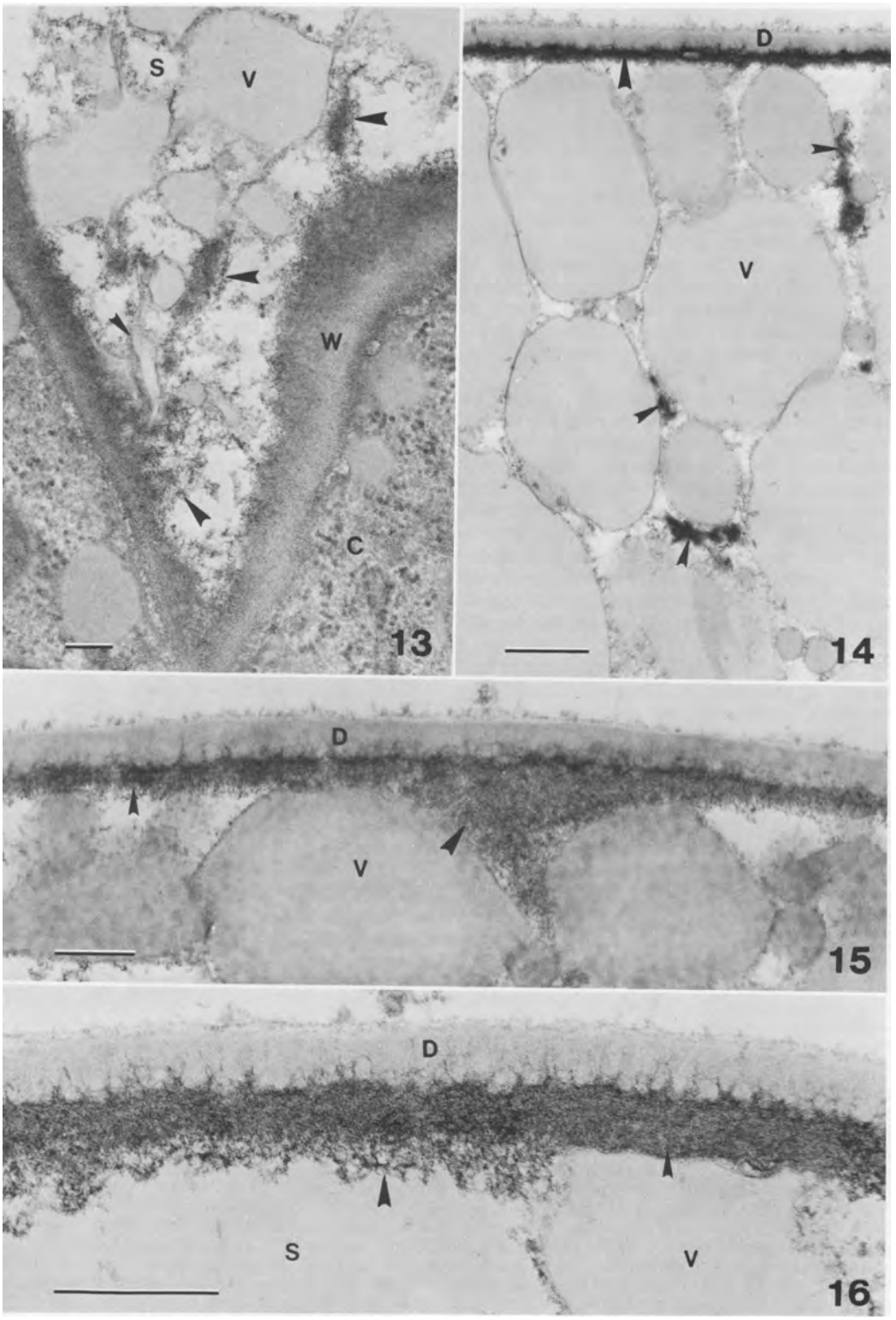
The subcuticular wall appeared more or less fibrous in character and loosely arranged in positions exposed to the hydrophilic compartment of the secretory cavity (Fig. 16). Wall material in the subcuticular wall region facing the secretory cavity wall appeared loosely aggregated compared to the more compacted region adjacent to the cuticle proper. At positions where a secretory vesicle pressed the fibrillar wall material against the cuticle, the subcuticular wall was more uniformly compacted parallel to the sheath surface and there was a suggestive laminar orientation of the deposited wall material.

Cell walls associated with formation of the secretory cavity underwent changes in thickness during glandular trichome development (Fig. 17). During presecretory stages of its ontogeny (stages 1–3), the cell wall progressively increased in thickness (curve A). The wall of disc cells showed little change in thickness during secretory cavity development and distension (stages 4–13, curve B). Thickness of the subcuticular wall (curve C) increased markedly during early stages of secretory cavity formation (stages 4–7), and continued to increase in thickness as the secretory cavity became greatly distended (stages 8–13). This nearly five-fold increase in wall thickness of the subcuticular wall, from 43 to 198 nm, originated by deposition of wall material derived from the disc cell wall, yet the disc cell wall retained a nearly constant thickness during development of the secretory cavity.

DISCUSSION

Presence of a cellulosic wall associated with the sheath of the noncellular secretory cavity was first reported from cytochemical studies of secretory glandular trichomes of *Cannabis* (Hammond and Mahlberg, 1978). Developmental studies of these glandular trichomes have focused attention on their gross form and the organization of the secretory cells (Schnepf, 1974; Dayanandan and Kaufman, 1976; Thomson and Healy, 1984; Owen, Benzing, and Thomson, 1988). Previous studies on organization of the secretory cavity described the accumulation of secretory products occurring between the cell wall and uplifted cuticle of the secretory cells (Bouquet, 1950; Schnepf, 1969; De Pasquale, 1974; Dell and McComb, 1975; Behnke, 1984). Our demonstration of a subcuticular wall in the secretory cavity of *Cannabis* trichomes contrasts with reports for organization of the dermal sheath of other glandular trichomes, and supports a polyphyletic interpretation for the origin of this cavity

Figs. 8–12 Secretory cavity development. **8.** Developing secretory cavity (S) showing enlarged hyaline areas in (large arrowhead) or about to enter (medium arrowhead) into cavity and origin of hyaline areas (small arrowhead) in more dense zone of wall. Cuticle present on cell wall (W). Bar = 0.2 μm. **9.** Somewhat enlarged secretory cavity (S) containing numerous hyaline areas of different sizes and configurations (small arrowheads) throughout secretory cavity. These areas arise from cell wall surface (W) to form rounded secretory vesicles (large arrowhead) in secretory cavity. Vesicles (arrowhead) are bound by a unit membrane (insert). C, secretory cell. Bar = 0.25 μm. Bar in insert = 0.1 μm. **10.** Periphery of secretory cavity (S) showing continuity of subcuticular wall (upper arrowhead) with wall (lower arrowhead) of disc cell (C). Wall components on both wall surfaces facing secretory cavity appear loosely structured. D, cuticle. Bar = 0.25 μm. **11.** Outer wall (W) surface of disc cell from a somewhat enlarged secretory cavity (S) showing origin of flattened hyaline areas (at and around medium arrowheads) from wall and their subsequent enlargement into more or less rounded vesicles (large arrowhead). Dense areas evident in wall (small arrowhead). Bar = 0.25 μm. **12.** Outer wall surface of disc cells (C) related to enlarged secretory cavity (S) showing loose fibrous character of wall surface (small arrowhead) and, at or near wall surface, presence of wall material (large arrowheads) in secretory cavity. Bar = 0.5 μm.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in glandular trichomes among angiosperms. Even in *Cannabis,* subtle differences in trichome development result in the formation of several types of glandular trichomes of different gross morphology (Hammond and Mahlberg, 1977). Such developmental differences for one species emphasize the difficulty to interpret homology between glandular trichomes or between diverse forms of secretory structures in angiosperms (Baas and Gregory, 1985). Intensive studies of glandular trichome development among angiosperms are necessary before we can formulate an evolutionary concept of the glandular trichomes.

A thickened subcuticular wall may function to provide the dermal sheath with greater structural strength than cuticle alone since this sheath spans a vastly greater unsupported surface area in the glandular trichome than any other structural feature within the plant. The surface area of the spherical secretory cavity will quadruple with doubling of its diameter during trichome development. The orientation of wall fibrils in the sheath parallel to its surface also may contribute to the structural rigidity necessary to retain an osmotic pressure which was observed to force secretory products out of a punctured secretory cavity (Lanyon, Turner, and Mahlberg, 1981).

Initial formation of the secretory cavity, revealing a fibrous character of the wall during the loosening process, resulted in a presumed hydrophilic compartment within the wall matrix. Hyaline areas and derived secretory vesicles appeared to represent a second, less polar, compartment containing electron-dense secretory products. The bounding membrane and its particulate components of secretory vesicles formed a third compartment associated with the secretory cavity. The composition of each compartment has not yet been determined although terpenes and cannabinoids are known to occur in the secretory cavity (Lanyon, Turner, and Mahlberg, 1981; Mahlberg, unpublished data). The released wall material was confined to the presumed hydrophilic compartment and not detected inside secretory vesicles.

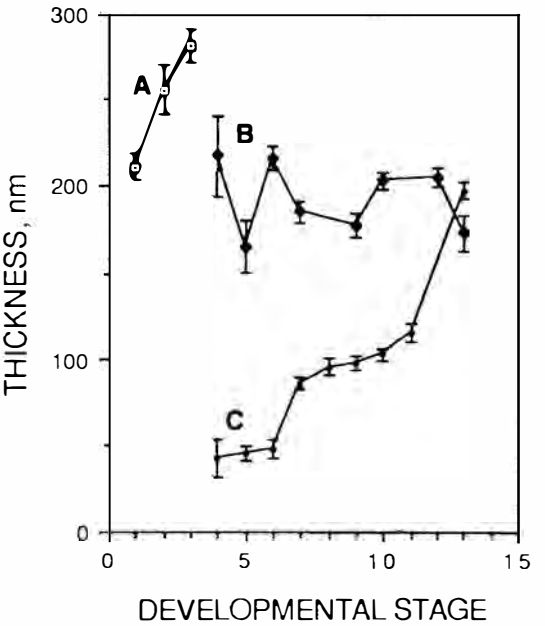

Fig. 17. Wall thickness of sheath and disc cells during glandular trichome development. Outer wall of immature secretory cells increased in thickness prior to secretory cavity initiation (curve A, stages 1–3). Disc cell wall showed no change in thickness (curve B) from time of initiation (stage 4) to maturation (stage 13) of secretory cavity. In contrast, subcuticular wall (curve C), a thin wall at initiation of secretory cavity (stage 4), increased five-fold in thickness to equal that of the disc cell wall (stage 13) during development of the secretory cavity. Vertical bar represents standard deviation for each measurement.

Development of the secretory cavity involved concomitant formation of secretory vesicles that initially appeared as membrane-bound structures in the wall. The flattened hyaline areas in the wall and the more round vesicles in the secretory cavity are interpreted to represent ontogenetic stages in the development of secretory vesicles in the enlarged glandular trichome. Since images of both flattened hyaline areas and more or less round vesicles were evident in a micrograph, the flat-

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Figs. 13–16. Subcuticular wall development. **13.** Fibrous character of outer surface of dense disc cell wall (W) of an enlarged secretory cavity, and presence of wall material (large arrowheads) in secretory cavity (S). Vesicles (V) of different sizes occur in secretory cavity including some of irregular shape closely associated with wall (small arrowhead). C, secretory cell. Bar = 0.25 μm. **14.** Enlarged secretory cavity showing wall material (small arrowheads) accumulated between secretory vesicles (V), some near wall under dermal sheath. Thickened cuticle (D) present above subcuticular wall (large arrowhead). Bar = 0.5 μm. **15.** Wall-cuticle sheath area showing wall material (large arrowhead) between secretory vesicles (V) aggregated with subcuticular wall (small arrowhead). D, cuticle. Bar = 0.25 μm. **16.** Wall-cuticle sheath area showing loosely arranged fibrous wall material along inner surface of wall (large arrowhead) facing secretory cavity (S) and somewhat compressed character of wall (small arrowhead) where wall is appressed to cuticle (D) by secretory vesicle (V). Wall appears laminated where it is appressed to cuticle (above small arrowhead). Bar = 0.25 μm.

tened shape was interpreted to be real, not an artifact of tissue processing. While some distortion in shape of round vesicles in the secretory cavity may have occurred in early stages of secretory cavity formation, it was less evident in mature trichomes reported here as well as in the literature where they appeared round in shape (Hammond and Mahlberg, 1977).

Origin of the particle-containing membrane that bounds secretory vesicles was unclear. Both features, membranes of hyaline areas and particles within the wall, possibly were derived from the dense bodies detected in the wall. Particle presence on the numerous secretory vesicles in small secretory cavities, and the appearance of numerous enlarged secretory vesicles in large secretory cavities, suggested a role in accumulation of secretory content in these vesicles.

The subcuticular wall increased in thickness throughout development of the secretory cavity. Several observations supported the interpretation that this thickening process resulted from wall matrix released from the disc cell wall surface: the fibrous material became evident along the subcuticular and disc cell wall surfaces from the time of initiation of the secretory cavity; fibrous material was most abundant along the disc cell wall surface and less so along the subcuticular surface; since secretion products moved into the cavity and away from the surface of the disc cells as the secretory cavity enlarged, the movement of fibrous material was interpreted to move with secretory products toward the subcuticular surface rather than counter to the direction of vesicle movement; and, the subcuticular wall became progressively thicker, whereas the disc cell wall did not thicken, during gland development.

Maintenance by disc cells of a uniformly thick wall concomitantly with the release of wall material from their surface throughout development of the secretory cavity suggested that new substrates were contributed to this growing wall by the disc cells. Cytochemical studies identified cellulose in association with the subcuticular wall (Hammond and Mahlberg, 1978). However, future studies may show the sheath wall to be composed of other wall components in addition to cellulose. Several endoglycanases are reported to be present in the growing cell wall (Fry, 1988), and such wall enzymes if present in disc cells could be associated with the release of diverse wall substrates into the secretory cavity. The composition of this wall matrix deposited into the secretory cavity and the role of disc cells in contributing to the membranes and particulate components associated with the hyaline areas in the wall remain to be investigated.

The release of wall material from the disc cell wall surface into the secretory cavity and the subsequent incorporation of this wall matrix into the developing subcuticular wall represent unique developmental phenomena for plant cells. Even more enigmatic is the occurrence of this process in a noncellular but growing structure, the secretory cavity. Further study will provide insight on developmental phenomena related to this structure and associated cells of glandular trichomes.

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