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ORIGINAL RESEARCH

Developmental Ultrastructure of Glandular Trichomes of *Rosmarinus officinalis*: Secretory Cavity and Secretory Vesicle Formation

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Abstract Glandular trichomes in the leaf lamina of *Rosmarinus officinalis* L. were examined by scanning and transmission electron microscopy. The leaves were characterized by an abundance of two types of glandular trichomes—small capitate and large peltate glandular trichomes. In addition to the glandular trichomes, numerous non-glandular trichomes were present on the abaxial surface of the leaf. These trichomes mainly predominated on the midrib, whereas glandular trichomes occurred on non-vein areas. At the initial phase of secretory cavity formation, hyaline areas were abundant in periclinal walls of head cells, while they were not observed in the anticlinal walls. The hyaline areas gradually increased in size, fusing with other areas throughout the wall. Loose wall material adjacent to hyaline areas was released from the head cell walls and migrated into the secretory cavities. As the secretory cavities continued to enlarge, the new vesicles emerging into the secretory cavities from the walls of head cells became surrounded with the surface of a typical membrane. They developed a round shape, but the contours of the vesicle surfaces appeared polygonal when tightly packed inside a cavity. These vesicles varied in size; small vesicles often possessed electron-dense contents, while large vesicles contained electron-light contents.

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Introduction

Glandular trichomes are generally accepted as the functionally specialized tissues that produce various secondary metabolites, which are then stored or volatilized at the plant surface. The unique characteristics of trichomes, or hairs, have traditionally been used as an important key in plant classification (Wagner 1991; Xiang et al. 2010).

While many plants use glandular trichomes to produce secondary compounds that are used for pollination, defense, and protection, among other things, several plant genera have been studied specifically for their potential use in industry. These include *Artemisia* (Polichuk et al. 2010), *Cannabis* (Marks et al. 2009), *Humulus* (Wang et al. 2008), *Mentha* (Turner et al. 2000), *Montanoa* (Robles-Zepeda et al. 2009), *Ocimum* (Iijima et al. 2004), *Salvia* (Baran et al. 2010), *Stevia* (Bondarev et al. 2010), *Tetradenia* (Gairola et al. 2009), *Zeyheria* (Machado et al. 2006), and *Rosmarinus* (Shabtay et al. 2008).

The large family Lamiaceae, which encompasses many aromatic species including *Rosmarinus*, has been studied because of the essential oils secreted by its members' glandular trichomes. In particular, the essential oil secreted by glandular trichomes of rosemary leaves has been used as an antiseptic, astringent, and food preservative for a long time (Pokorny 2008). These glandular trichomes of the genus *Rosmarinus* are major accumulating sites for various secondary metabolites that have the helpful properties of inhibiting skin tumorigenesis (Huang et al. 1994), exhibiting antioxidant activity (Richheimer et al. 1999), protecting

red blood cells (Haraguchi et al. 1995), and exhibiting antileukemic activity (Shabtay et al. 2008).

Glandular trichomes are often classified morphologically into two main types—peltate and capitate—and can be distinguished by head size and stalk length (Ko et al. 2007; Baran et al. 2010). Peltate trichomes have a short stalk and a large head, containing 4–18 cells; capitate trichomes have a stalk that is twice as long as their head (Ascensao and Pais 1998). Peltate trichomes have broad secretory cavities, 40–60 μm in diameter, and capitate trichomes have globular-like secretory cavities, 10–30 μm in diameter (Luo et al. 2010).

In our study, two types of glandular trichomes, peltate and capitate, and non-glandular trichomes were investigated on the leaves of *Rosmarinus officinalis* by light microscopy. While the volume density and distribution of the distinct types of glandular trichomes, found using stereological and histochemical techniques, have been previously reported (Marin et al. 2006), the ultrastructural aspects of glandular trichomes of rosemary had not yet been investigated clearly.

This paper examines the developmental ultrastructure of the glandular trichomes of rosemary at the scanning electron microscopy and transmission electron microscopy levels. Special emphasis has been placed on the secretory cavity and vesicles because they contain the distinctive structural and functional features of glandular trichomes. Our objectives also included determining the origin and early development of the secretory products, the pattern of compartmentalization of components in secretory cavities, and the origin of subcuticular cell walls.

Materials and Methods

Mature leaves between the third and tenth nodes were harvested from *R. officinalis* stems grown under greenhouse conditions at Konkuk University. Leaf segments were fixed with 2% glutaraldehyde in a 0.1 M sodium phosphate buffer (pH 7.2), at 4°C for 4 h, and post-fixed for 2 h in 1% unbuffered osmium tetroxide.

For SEM examination, samples were then fixed with 2% (*v*/*v*) glutaraldehyde and 1% OsO_4 for 2 h at room temperature. They were dehydrated with a graded ethanol series and then dried to their critical point with solvent-substituted liquid carbon dioxide. After coating with a thin layer of gold in a sputter coater, the samples were observed with a field emission scanning electron microscope (JSM-6700F, JEOL).

For TEM examination, samples were fixed with 2% (*v*/*v*) glutaraldehyde and post-fixed with 1% osmium tetroxide aqueous solution for 2 h at room temperature. The materials were dehydrated with a graded ethanol series and then embedded in Spurr's low viscosity resin. Ultrathin sections were stained with uranyl acetate and lead citrate and photographed using a transmission electron microscope (JEM-2000EXII, JEOL) at 80 kV.

Results

Aspects of Distribution and Structure

Two morphologically distinct types of glandular trichomes, capitate and peltate, occurred on *R. officinalis* leaves. The adaxial surface had a relatively flat appearance when viewed by SEM. There were very few non-glandular and peltate glandular trichomes on the leaf lamina. Capitate glandular trichomes were not examined on the adaxial surface (Fig. 1a). On the abaxial surface, however, both capitate and peltate glandular trichomes were densely distributed on the lamina. Non-glandular trichomes particularly appeared on the leaf midrib and major veins and were multicellular with a stellate shape and sharp-pointed tips (Fig. 1b).

The small capitate glandular trichomes consisted of a globose unicellular head attached to the leaf with a two- or three-celled uniseriate stalk. The stalks had a length of 8–10 μm and the heads had a diameter of 13–15 μm (Figs. 1c and 3b). Epicuticular wax crystals, which are net-like structures, were distinctly present in the abaxial surface, whereas they were not observed at all in the adaxial surface (Fig. 1d).

The peltate glandular trichomes each consisted of a large eight-celled head, with an enlarged secretory cavity, attached to a two-celled short stalk. The heads of the peltate trichomes had a diameter of 60–85 μm, and the stalks had a length of 8–10 μm (Figs. 1e, f and 2a). A cuticular sac that was detached from the trichomes represented an external feature of mature head cells. The cuticular sac of the most mature peltate trichomes was often partially disclosed (Fig. 1f) or entirely removed from the head cells (Fig. 2a). Subcuticular sacs appeared to be hardened by cuticles that ruptured partially or entirely under the effect of environmental pressure (Fig. 2b, c). The peltate glandular trichomes revealed the internal structure of secretory cavities, which contain lots of membrane-bounded vesicles (Fig. 2d).

As the glandular trichomes continued to grow, the secretory vesicles also grew, and eventually each secretory cavity was packed with them. The surfaces of the vesicles exposed in the cavities were bounded by distinct membranes, which became continuous with that portion of the membrane, delimiting vesicle surfaces in the cavities. These vesicles were round in shape, but varied in diameter size from 1.5 to 7.5 μm (Fig. 2d–f). Organization of the membranes at the vesicle–subcuticular wall interface

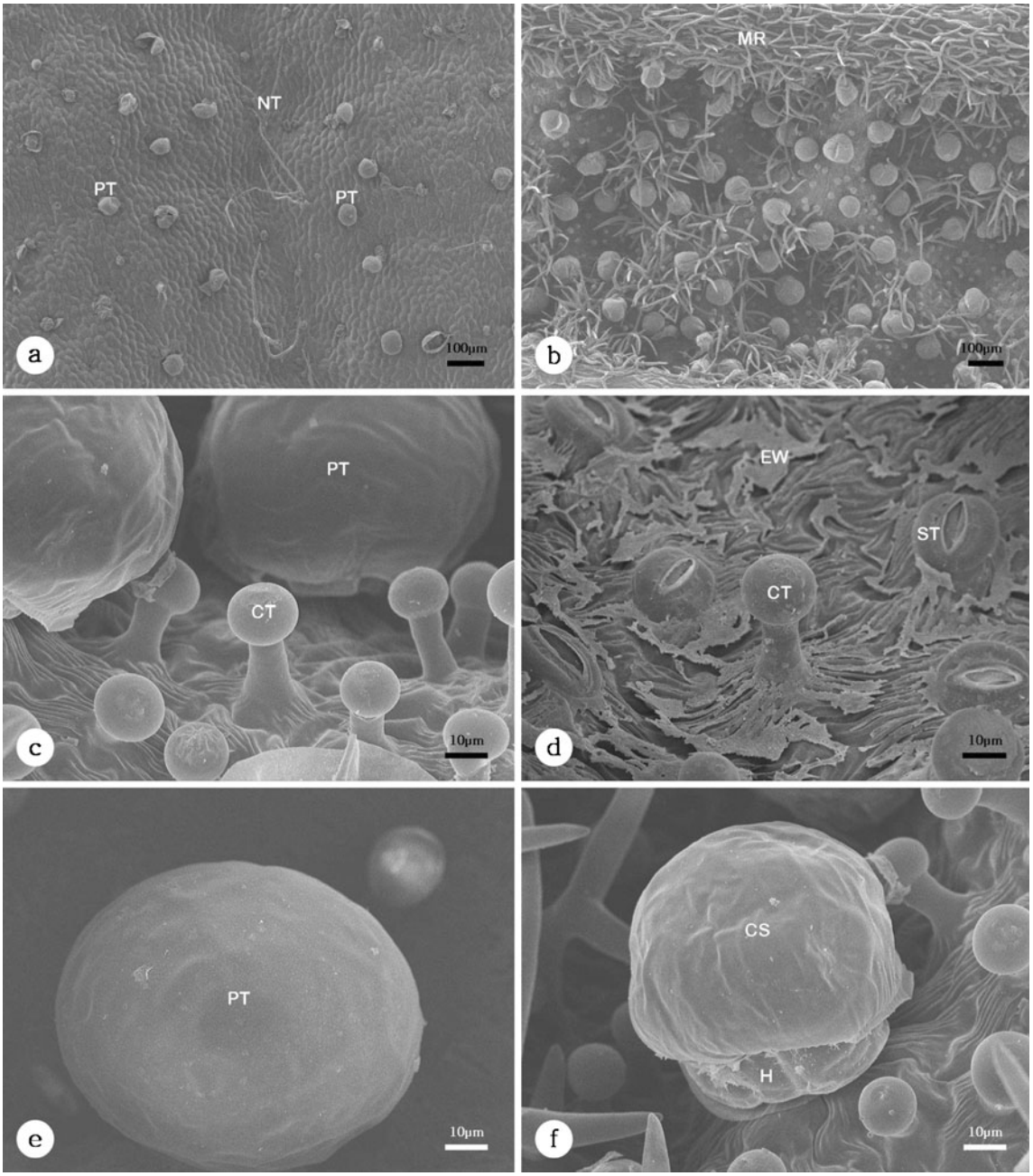

Fig. 1 Scanning electronic microscopic micrographs of leaf lamina in *R. officinalis*. **a** Peltate trichomes (*PT*) and non-glandular trichomes (*NT*) are scattered throughout the adaxial leaf surface. **b** The abaxial surface of a leaf shows numerous peltate and capitate trichomes, as well as non-glandular trichomes on the midrib (*MR*). **c** Detailed view of peltate (*PT*) and capitate (*CT*) trichomes on the adaxial leaf surface. **d** A capitate trichome (*CT*) surrounded with stomata (*ST*) is shown; epicuticular wax (*EW*) on the epidermis is apparent. **e** A mature peltate gland (*PT*). **f** Detailed view of a peltate trichome beginning the rupture of cuticle and mature peltate trichome after the splitting of the cuticular sac (*CS*)

showed a continuous surface, and remnants of vesicle membranes were often observed on the subcuticular walls when the secretory sac ruptured (Fig. 2f). Both peltate and capitate trichomes during the early phase of glandular trichome morphogenesis contained abundant cytoplasm, including prominent nucleus, mitochondria, polysomes, small vacuoles, and plastids (Fig. 3a–c).

Aspects of the Formation of Secretory Cavities

During the early stages of secretory cavity development, the wall loosening process occurred within the periclinal walls and was not observed in the anticlinal walls of head cells. Hyaline areas, electron-light regions in the walls, also contributed to the separation of the subcuticular walls and

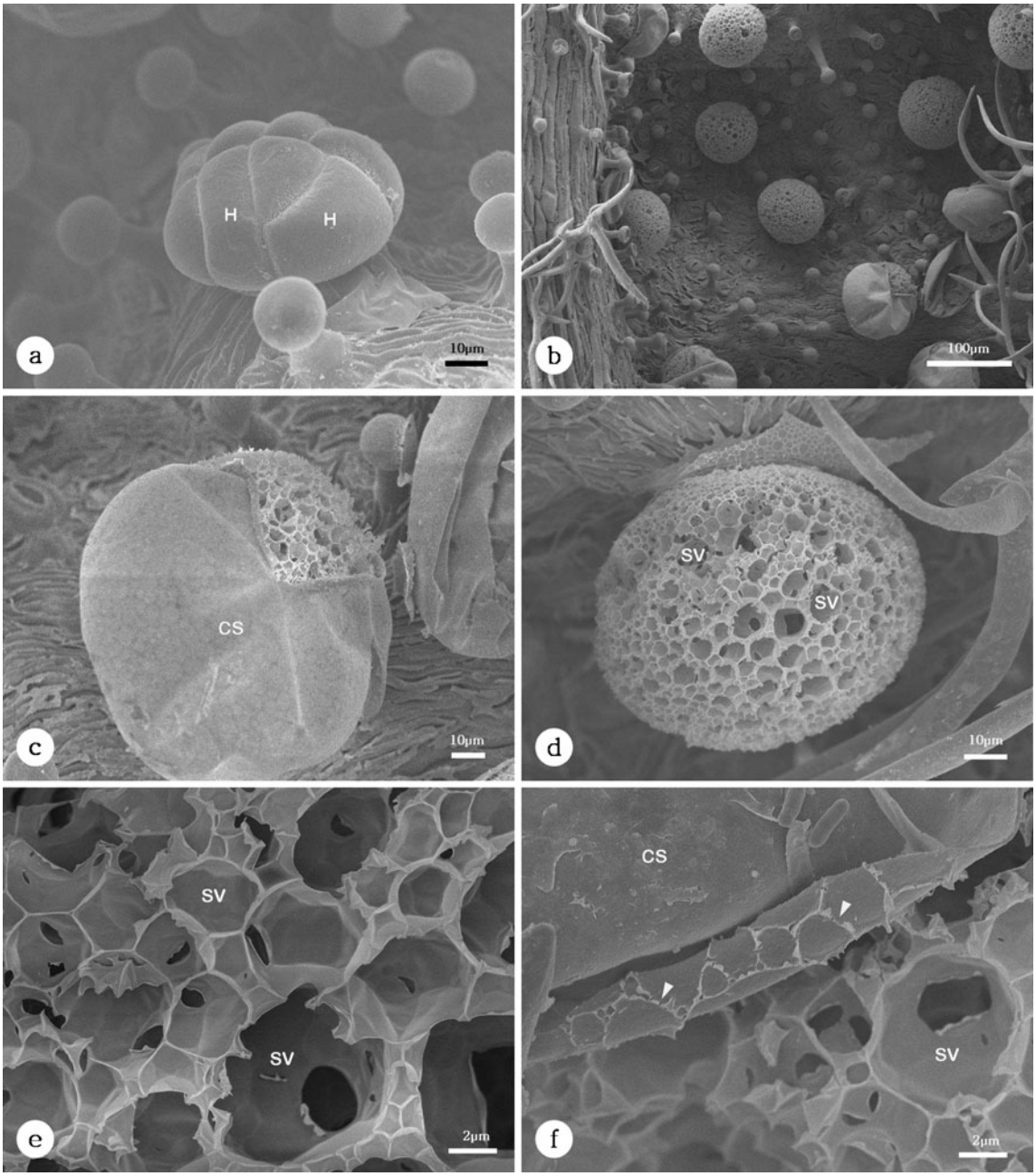

Fig. 2 Scanning electronic microscopic micrographs of leaf lamina in *R.* officinalis. **a** The rupture of the cuticular sac (*CS*) of a peltate trichome reveals eight head cells (*H*). **b** Peltate trichomes' detached cuticular sacs and capitate trichomes are shown in the central region between leaf veins. **c** A mature peltate trichome with partially detached cuticular sac (*CS*) shows inner secretory vesicles in the cavity. **d** An entirely disclosed peltate trichome shows whole secretory vesicles (*SV*). **e** Detailed view of secretory vesicles (*SV*). **f** The remnants of vesicle membranes (*arrowheads*) are shown when the ruptured cuticular sac (*CS*) is upside down

the formation of secretory cavities (Fig. 3d). At the initial phase of cavity development, the loose wall matrix separated from the wall surfaces of the head cells and actively extended into the secretory cavities; its origins were similar to that of vesicles formed by the plasma membranes of head cells (Fig. 3e, f). Also during the early phase of secretory cavity formation, a few small vesicles appeared; wall materials associated with the vesicle surfaces dispersed in the secretory cavities (Fig. 4a).

Aspects of the Formation of Secretory Vesicles

Secretory vesicle development was associated with the formation of membranes along the walls facing the cavities.

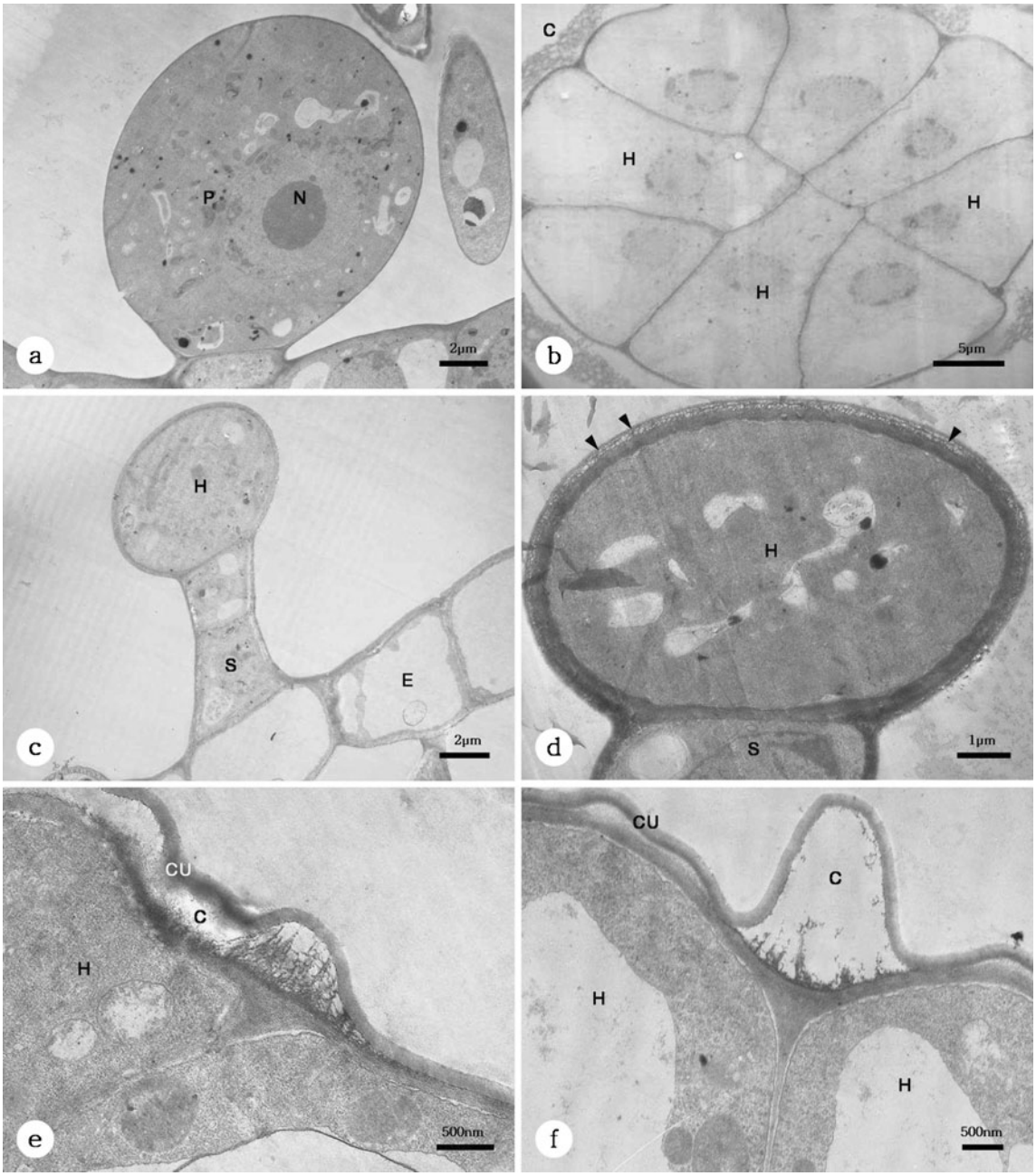

Fig. 3 Transmission electronic microscopic images of glandular trichomes of *R. officinalis*. **a** A young peltate trichome shows dense cytoplasm, including prominent nucleus (*N*), plastids (*P*) with electron-dark plasoglobuli, and numerous mitochondria. **b** A transverse section of a mature peltate trichome shows eight head cells (*H*). **c** A young capitate trichome with a head (*H*) and two-celled stalk (*S*) on the leaf lamina. **d** A capitate trichome showing initiation of a secretory cavity; numerous hyaline areas (*arrowheads*) are distinctly present in the wall at the early phase of secretory cavity development. **e** Fibrous wall material released from the head cell is shown in the young secretory cavity (*C*) at the initial phase of cavity formation. **f** A loose wall matrix extending into the secretory cavity

This membrane formation was preceded by the appearance of electron-dark bands in the walls. The dark bands were observed as fragments throughout the walls and became linearly arranged in the walls as a membrane form (Fig. 4b). The mottled wall regions often distributed on the thickened walls or juncture regions between head cells. These wall components probably contributed to the formation of numerous small secretory products in the cavities (Fig. 4c).

At the mature phase of cavity development, secretory vesicles that were released from the wall surfaces of head cells gradually aggregated in the secretory cavities. Secre-

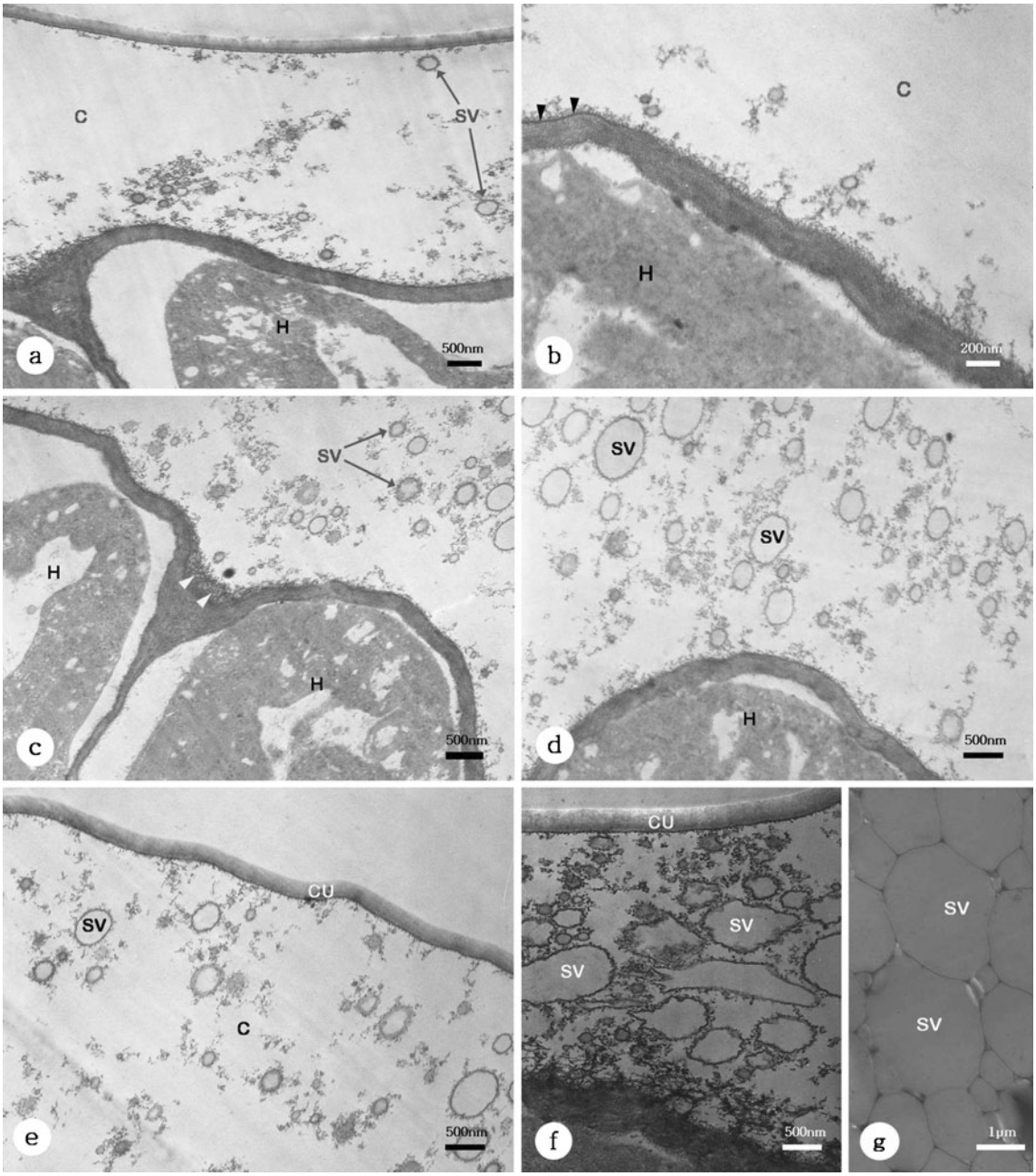

Fig. 4 Transmission electronic microscopic images of glandular trichomes of *R. officinalis*. **a** A dispersed wall matrix contacts small secretory vesicles in an enlarged secretory cavity (*C*). **b** A loose wall matrix from the wall surface enters the secretory cavity. Note the electron-dark band of wall material (*arrowheads*) that appeared at the wall–cavity interface. **c** A mottled wall (*arrowheads*), compressed in shape, often appears in the juncture region between adjacent head cells. **d** Secretory vesicles (*SV*) released from the wall surface of head cells aggregate in the secretory cavity. **e** Secretory vesicles (*SV*) containing electron-light or electron-dense substances are deposited in the secretory cavity. These vesicles are delimited by cuticle (*CU*) and subcuticular wall. **f** Secretory vesicles (*SV*) surrounded by membranes with fibrillar material are aggregated in the cavity. Thin subcuticular wall is present along the cuticle (*CU*). **g** Detailed view of secretory vesicles (*SV*) packed in the cavity

tory products passed through the walls to deposit in the cavities as membrane vesicles (Fig. 4d), and as new secretory vesicles were deposited in the secretory cavities, existing vesicles were redistributed throughout (Fig. 4e). With the growth of the secretory cavities, secretory vesicles of different sizes were observed. These vesicles typically possessed dense or loose contents and were surrounded by a membrane with fibrillar material. Electron-dense contents appeared in the small vesicles, while electron-light contents were observed in large vesicles (Fig. 4f). These secretory vesicles developed a more or less round shape; however, the contours of the

vesicle surfaces appeared polygonal when they were tightly packed inside a cavity (Fig. 4g).

Discussion

Aspects of Distribution and Structure

Peltate and capitate trichomes appear with a variable number of head cells, ranging from 4 in *Leonotis leonurus* (Ascensao et al. 1995) to 8 in *Mentha piperita* (Turner et al. 2000) and *Zeyheria montana* (Machado et al. 2006) and to 12 in *Calaminta menthifolia* (Hanlidou et al. 1991) and to 18 in *Micromeria fruticosa* (Werker et al. 1985). Peltate trichomes have common characteristics in structure and morphology across genera. They usually consist of a vacuolate basal cell with a short stalk and a cytochemically dense head with secretory cells (Turner et al. 2000; Machado et al. 2006). The peltate and capitate glandular trichomes on *R. officinalis* leaves expectedly showed the same structural features with that of other plants. The head cells of *R. officinalis* glandular trichomes had common characteristics such as dense cytoplasm, numerous mitochondria, plastids with plastoglobuli, and well-developed endoplasmic reticulum.

Aspects of the Formation of Secretory Cavities

A secretory cavity is a large depository that is formed above secretory cells and accumulates the secretion products. Their general origin and development, as well as that of the subcuticular walls, were previously described in glandular trichomes of *Cannabis* (Kim and Mahlberg 1991, 1995; Mahlberg and Kim 1992, 2004) and *Hummulus* (Kim and Mahlberg 2000). In rosemary leaves, secretory cavities of glandular trichomes arise by the splitting of the outer walls of head cells to form non-cellular compartments into which head cells deposit secretory products for cuticular sac development during cavity development.

The formation of secretory cavities begins with loosening wall material that becomes fibrous in appearance. Hyaline areas, which represent electron-light regions along the inner region of the wall, gradually increase. This wall loosening and separation process evidently contributes to the formation of subcuticular walls.

In *Cannabis*, the outer walls of secretory cells split tangentially to initiate intrawall cavities (Kim and Mahlberg 1991, 2000; Mahlberg and Kim 1991). Like *Cannabis*, the secretory cavities of rosemary enlarge as secretions are accumulated in them. The outer portions of the walls remain associated with the cuticle to form subcuticular walls. The cuticle and subcuticular walls increase in thickness as secretory cavities enlarge.

Aspects of the Formation of Secretory Vesicles

Secretory vesicle formation is associated with electron-dense secretions formed in abundance in the secretory cells. According to Mahlberg and Kim (1992, 2003), secretory vesicles contribute to the formation of cuticle and subcuticular walls during secretory cavity development. These authors proposed that the fibrils originate from the outer bilayer of the plasma membrane because of their abundance and distribute as fibril matrices throughout the cell walls and the intervesicular zone.

In glandular trichomes of *R. officinalis* leaves, numerous vesicles of different sizes are continuously formed throughout the head cell walls during glandular trichome development. At the initial phase of formation of vesicles, electron-dark bands in the walls of head cells were observed throughout as fragments. The bands became linearly arranged in the walls as a membrane formed. We speculate that these bands contribute to the formation of the vesicular membrane. Secretory products passed through the walls to deposit as membrane vesicles in the cavities. The mottled wall was interpreted to be numerous tiny electron-light quantities of secretory products. This phenomenon appeared to occur along the entire wall surface, whether associated with the wall surface or distant from it.

As the glandular trichome continued to enlarge, the secretory vesicles became larger in size and more tightly packed inside the secretory cavities. Organization of the membranes at the vesicle–subcuticular wall interface formed a continuous surface at this interface. The remnants of vesicle membrane were often observed on the subcuticular walls when the secretory sac ruptured. This unique phenomenon is interpreted to imply that rapid migration of numerous membrane vesicles into secretory cavities gives rise to the formation of globular secretory vesicles. Secretory vesicles of different species contain distinctive substances such as fatty acids, alkaloids, phenols, volatile monoterpenes, diterpenes, and sesquiterpenes, all of which contribute to plant fragrance (Kim and Mahlberg 1997; Turner et al. 2000; Mahlberg and Kim 2004; Machado et al. 2006; Robles-Zepeda et al. 2009). The histochemical study of rosemary revealed that phenolic compounds are found only in peltate trichomes and not in capitate trichomes (Marin et al. 2006).

We assume that evaporation from glandular trichomes, representing continued loss of monoterpenes from cavities, may contribute to the continued production of secretory vesicles at head cell wall surfaces. This point provides a foundation for further research into the relationship between secretory vesicles and secretion mechanisms in glandular trichomes. However, it remains unknown whether secretory vesicles in cavities with different electron densities contain the same compounds. The contents of secretory cavities of

individual glandular trichomes should be collected and gas chromatographically analyzed for further understanding.

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