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Anatomy and Ultrastructure of Epidermal Cells in the Haustorium of a Parasitic Flowering Plant, *Cuscuta japonica*, during Attachment to the Host

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Changes of epidermal cells in the haustorium of the parasitic *Cuscuta japonica* during its attachment to the host plant *Impatiens balsamina* were studied with light and electron microscopy. In the transverse sections of dodder stems not in contact with the host, epidermal cells had rounded outlines. However, when haustorial initials developed in the cortex of the parasite stem at the contact site, the epidermal cells had more dense cytoplasm and conspicuous nuclei than before, and their outline was flat in the longitudinal section. As meristem cells developed from those initials, the epidermal cells became more elongated. When the haustorium was fully matured, the apical tips of the elongated epidermal cells at the contact site branched like toes, producing numerous projections via cell wall invaginations. This event caused spaces to form between the projections; coincidently, the surface area of the apical ends of the epidermal cells increased. The dense cytoplasm at those projections contained prominent nuclei and abundant other organelles, suggesting a active metabolism. Osmiophilic particles, releasing into the cell walls from the cytoplasm, were though to be associated with the loosening and elongating of the epidermal cell walls. Dense and homogeneous materials were secreted within the spaces between the projections. These materials could play an important role in cementing the haustorium onto the surface of the host organ.

Keywords: anatomy, *Cuscuta japonica*, dodder, epidermal cells, parasitic angiosperm, ultrastructure, upper haustorium

Parasitic weed dodders (*Cuscuta* spp.) are found worldwide, both in cultivated regions and in areas that are not cropped (Kuijt, 1969; Dawson et al., 1994). They parasitize a wide range of host species (Dawson et al., 1994). This parasitic ability suggests that dodders have a variety of adaptive mechanisms for host attachment (Vaughn, 2002). The parasitic organs in the *Cuscuta* are divided into two parts: the upper haustorium, or adhesive disks, and the endophyte (Kuijt, 1977). The former is the haustorial portion lying external to the host; the latter invades the host. Most research on the structure of *Cuscuta* has concentrated on the endophytes rather than the upper haustoria (Kuijt, 1977). Thus the attachment mechanism(s) of the upper haustoria are not known in detail. Field and laboratory investigations have found that many haustoria fail to make functional attachments (Baird and Riopel, 1983; Lee and Lee, 1989; Lesny, 1991). In several parasites, this contact is undoubtedly promoted by the tight adhesion of the upper haustoria to the host surface, thereby reinforcing the subsequent thrust of the invading endophyte (Riopel and Timko, 1995).

With regard to *C. odorata*, Weinert and Barckhaus (1975) have stated that cuticular material occurring at the interface of the parasite and host may act in cementing the parasite to the host. In *C. reflexa*, the cementing substance that is present between the parasite and the host is a complex mixture of sticky secretions from the parasite's epidermal cells (Heide-Jørgensen, 1987). The adhesive cutinaceous material in *Viscum minimum* and the adhesive polysaccharide in *Cassytha pubescens* are secreted from the epithelial trichomes (Heide-Jørgensen, 1989). Although Lee and Lee (1989) have described the structural development of an early-stage of upper haustorium in *C. australis*, they do not mention the epidermal cells in detail. In *C. pentagona*, the elongated epidermal cells (trichomes) of the parasite stem release electron-dense particles (cell wall-loosening complexes) into the cell walls, and the trichomes secrete pectinaceous cementing material onto the parasite-host interface (Vaughn, 2002). In many root-parasitic weeds, a polysaccharide substance is involved in the production of that cementing material (Jeol and Losner-Goshen, 1994; Losner-Goshen et al., 1998; Neumann et al., 1999).

The shoot sub-apical cells of light-grown *Cuscuta japonica* seedlings, developed from embryos in which the cells contain numerous reserves (Lee, 2006), have chloroplasts possessing thylakoids well-organized into grana, suggesting a capacity for photosynthesis (Lee, 2007a, b). After *C. japonica* seedlings contact the host, the upper haustorium develops through three main stages of the haustorial initials, the meristem, and the endophyte primordium (a host-penetrating tissue) in the middle layer of the cortex in the parasite stem. For this, the current author has briefly described the modification of epidermal cells in the mature upper haustorium (Lee, 2007c). The aim of the present study was to examine structural changes in those epidermal cells, with respect to host attachment, from the upper haustorium of *C. japonica*.

MATERIALS AND METHODS

Plant materials

Mature dry seeds of dodder (*Cuscuta japonica* Choisy) were scarified with concentrated sulfuric acid for 45 min,

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then rinsed in tap water followed by distilled water. They were placed on moist filter paper in Petri dishes and germinated in an incubator in the dark at 30°C, where they further developed into seedlings. The roots of 3-day-old dark-grown seedlings were wrapped with wet cotton, put into 500-mL covered beakers, and placed near windows for exposure to sunlight for 3 d. The tip regions of these 6-day-old seedling shoots, when placed in contact with the host plant *Impatiens balsamina* L., entwined the host stem and produced upper haustoria on the side of the dodder stem that touched the host. Light and electron microscopy were used to examine these shoot-tip regions of free-living 6-day-old dodder seedlings as well as their tissues at subsequent developmental stages of upper haustoria in the parasite stem.

Light and Transmission Electron Microscopy

Seedling tissues were sliced into approximately 1 mm^3 segments and pre-fixed in a mixture of 2.5% glutaraldehyde-2% paraformaldehyde in 0.1 M sodium cacodylate

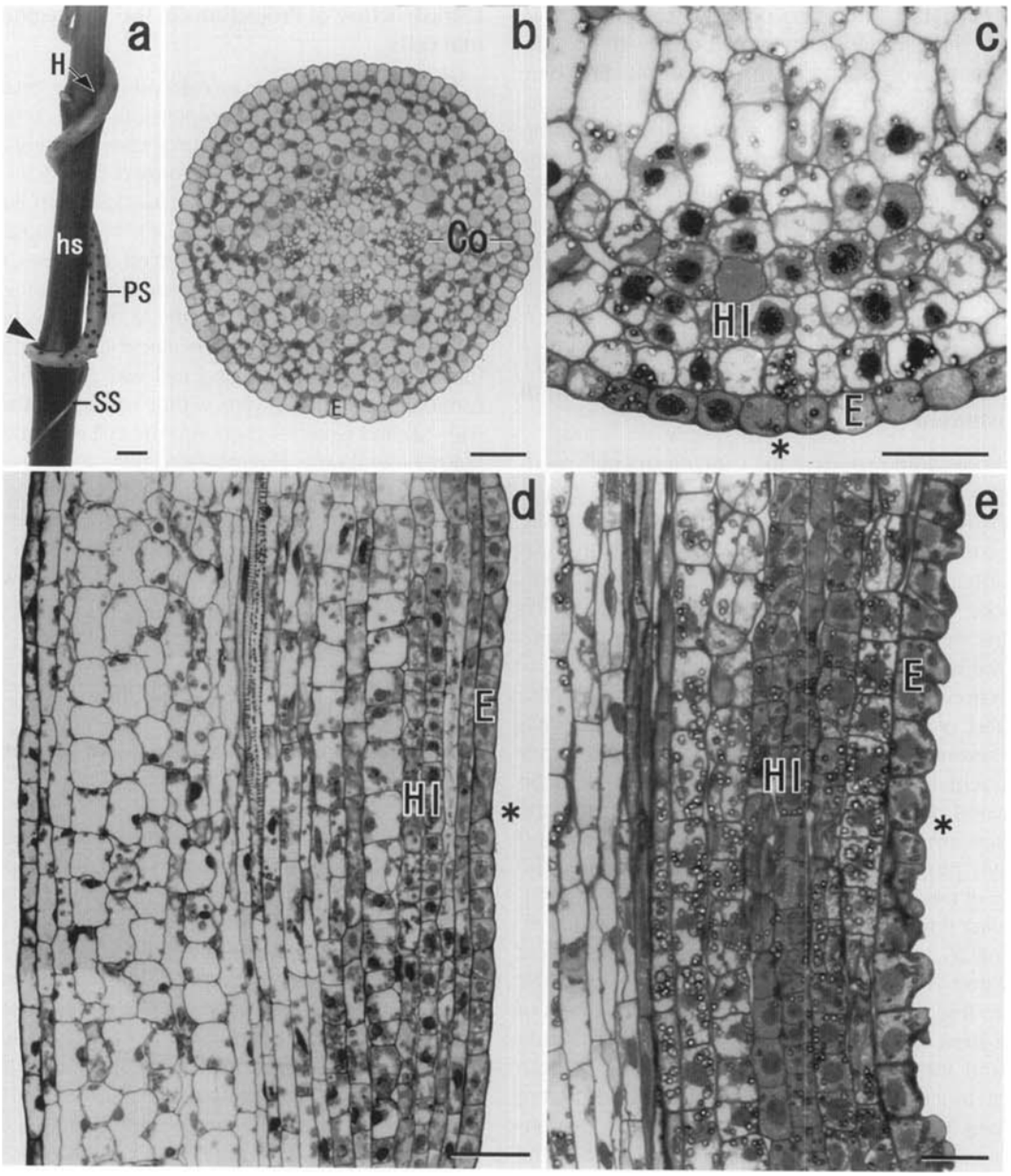

Figure. 1. Morphology of parasite (*Cuscuta japonica*) growing on host (*Impatiens balsamina*) stem (**a**) and light micrographs of epidermal cells during early development of upper haustorium (**b-e**). (**a**) Parasite stem (PS) entwining host stem (hs). After a thin seedling shoot (SS) of the parasite coils the hs, primary haustoria (arrowhead) develop from seedling stem at contact site. Shoot tip grows further and becomes thick parasite stem (PS). Haustoria (H) secondarily develop at contact site of thick PS. Bar = 25 µm. (**b**) Transverse section of parasite stem not in contact with host comprises one-layered epidermal cells (E) and six- to seven-layered, vacuolated cortical cells (Co). Bar = 50 µm. (**c, d**) In first stage of contact between parasite and host, in transverse (c) and longitudinal sections (**d**), haustorial initials (HI) develop in mid-cortex of parasite stem. Epidermal cells (E) contain more dense cytoplasm and evident nuclei than before contact. They are round in transverse sections (c), and rectangular in longitudinal sections; outline of surface is flat (**d**). Bar = 25 µm in (c), 50 µm in (d). Asterisks (*) indicate sites of host contact. (**e**) Epidermal cells are more or less elongated toward contact site (*). Haustorial initials (HI) have dense cytoplasm, prominent nuclei, and numerous starch grains, and show division activity. Bar = 50 µm.

buffer (pH 6.8) for 2 to 3 h at room temperature. Those segments were then exposed twice to microwave radiation for 10 and 20 s at 70% of maximum power in an 800-W Pelco Model 3450 Laboratory Microwave Processor (Ted Pella, Inc., Redding, CA, USA) that was equipped with a thermistor copper temperature probe and an auxiliary Pelco 3420 Microwave Load Cooler (Ted Pella, Inc.). The tissues were post-fixed in 1% osmium tetroxide, buffered at pH 6.8, and microwaved three times, for 40 s each. They were then washed in buffer and dehydrated in a graded acetone series in the microwave oven at 37°C. The tissue pieces were then infiltrated and embedded with Spurr's resin (Spurr, 1969). Thick sections that were first cut with an LKB-V ultramicrotome were stained with 0.05% toluidine blue and examined under an Olympus BH2 light microscope. Thin sections that were cut with an RMC MT-7000 ultramicrotome were mounted on grids and stained with uranyl acetate and lead citrate. They were examined and photographed with JEM 100 CXII or Hitachi H-7600 transmission electron microscopes at 80 kV.

RESULTS

Anatomy of the Epidermal Cells During Development of Upper Haustorium

After the hooked tip regions of the *Cuscuta japonica* seedlings were placed on the host stem, they entwined it, and the upper haustoria primarily developed from the parasite stem at the contact site (Fig. 1a). The shoot tips of the parasite grew further on the host stem, and the parasite stems became thicker in diameter than the seedling shoots, which withered after being parasitized. Those thick parasite stems also coiled the host stem, producing secondary haustoria.

A cross section of the *Cuscuta* stem that did not touch the host consisted of one-layered vacuolated epidermal cells and six- to seven-layered cortical cells (Fig. 1b). After contact, subsequent changes to the epidermal cells could be described based on three main developmental stages of the upper haustorium: the haustorial initials, the meristem, and the endophyte primordium (a host-penetrating tissue) in the middle layer of the cortex in the parasite stem (Lee, 2007b). During the first stage of contact between parasite and host, haustorial initials with a dense cytoplasm and prominent nuclei appeared in the middle layer of cortical cells from the parasite stem (Fig. 1c-d). Meanwhile, the epidermal cells of the parasite stem at the contact site began to show dense cytoplasm and more evident nuclei compared with those that did not touch the host. These epidermal cells were round in their transverse section (Fig. 1c). They demonstrated division activity and a rectangular appearance in the longitudinal section, and the outline of their surface was flat (Fig. 1d). As the haustorial initials started to divide actively, the epidermal cells gradually elongated toward the contact site (Figs. 1e, 2a-b). At this stage, the initial cells of the haustorium and the epidermal cells contained many more starch grains than before.

In the second stage of contact, a group of meristematic cells developed from the haustorial initials. Simultaneously, the epidermal cells elongated even more, and their nuclei and dense cytoplasm were distributed in the tip regions (Fig. 2c). As the meristem became more evident, the apical ends of the epidermal cells had a branched appearance (Fig. 2d). In the final stage of contact, haustorial maturation progressed and upper haustoria protruded on the parasite stem at the contact site. As the upper haustorium fully matured, an endophyte primordium (EP) developed from the meristem cells. This EP, a host-invading tissue, consisted of file cells and digitate cells. Concurrently, the epidermal cells produced numerous projections at the apical ends (Figs. 3a-b).

Ultrastructure of Projections in the Tip Region of epidermal cells

The cell walls at the apical ends of the epidermal cells were folded into toe-like projections that created crevices (Figs. 3c-d, 4c-d). One large projection had invaginated further and smaller projections formed (Fig. 3c). The projections from neighboring cells interlocked with each other at the crevices (small stars in Fig. 3c). The cytoplasm of those projections contained numerous cell organelles, e.g., dictyosomes, mitochondria, polysomes, and rough endoplasmic reticulum (r-ER) (Figs. 3c, 4c-d). At the projections, a large number of osmiophilic or very electron-dense particles were found in the cytoplasm and cell wall (Figs. 3d, 4a-d). The osmiophilic particles were within vesicles in the cytoplasm (Fig. 4a) and were released into the cell wall just outside the plasma membrane (Figs. 4b-c). Slightly dense, homogeneous material accumulated in the spaces between the projections and at the interface between the parasite and the host (Figs. 3c-d, 4c-d). Within the cytoplasm at the tips of the epidermal cells, many dictyosome-derived vesicles were distributed near the cell walls (Figs. 4c-d).

DISCUSSION

Cellular Response of Parasite Stem in Early Contact Stage

In the first stage of contact between the parasite and the host, vacuolated parenchymatous cells of the epidermis and the mid-cortex in the parasite stem began to de-differentiate at the contact site; a dense cytoplasm, conspicuous nuclei, and numerous starch grains appeared in these cells. Subsequently, they divided. Such a cylogogical feature is also found in the early development of the upper haustorium in *C. australis* (Lee and Lee, 1989). This cellular response and subsequent division, as well as recognition of the direction of elongation in the epidermal cells, may be triggered by tactile stimuli when the *Cuscuta* stem contacts the host surface (Lee, 2007c). When the upper haustorium of *C. australis* does not touch its host, a functional, mature upper haustorium with a host-penetrating tissue, i.e., the endophyte primordium, does not develop (Lee and Lee, 1989). Tada et al. (1996) also have reported that contact stimuli induces the haustorium of *C. japonica*. Starch grains that accumulate in the epidermal and mid-cortical cells of the parasite stem at the contact site may be used as an energy source for various cellular activities, including cell division and elongation, during the development of the mature

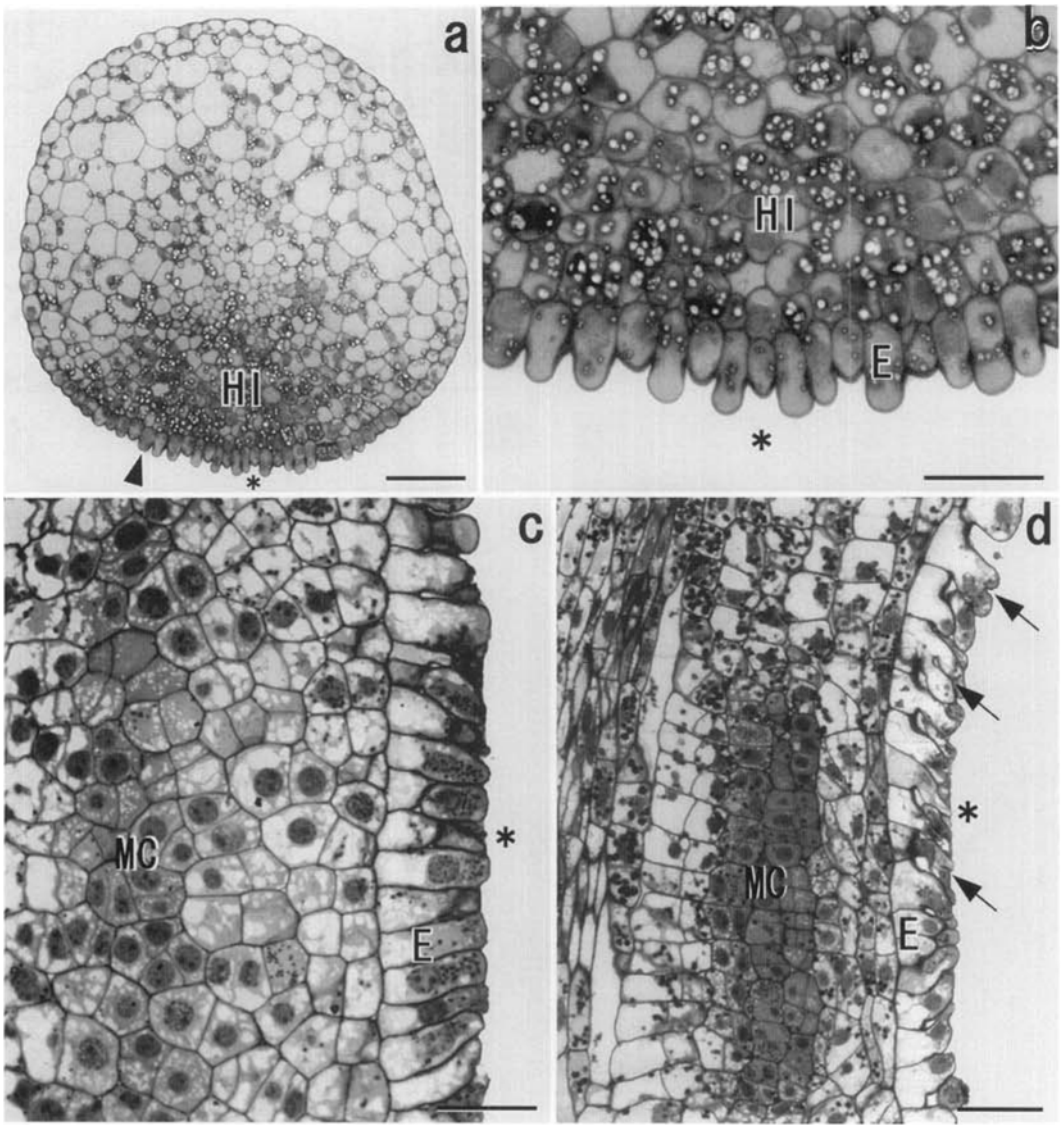

Figure 2. Light micrographs of elongating (**a-c**) and branching epidermal cells (**d**). Asterisks (*) indicate sites of host contact. (**a**) Epidermal cells are more elongated (arrowhead) than those in Fig. 1e. HI, haustorial initials. Bar = 50 μm. (**b**) Magnified view shows elongated epidermal cells (E) and haustorial initials (HI) with dense cytoplasm, prominent nuclei, and numerous starch grains. Bar = 25 μm. (**c**) In transverse section showing meristematic cells (MC), epidermal cells (E) are elongated toward contact site (*), and contain dense cytoplasm and large nuclei restricted to tip regions. Bar = 25 μm. (**d**) In longitudinal section of distinct meristem cells (MC), epidermal cells (E) are branched at tip regions (arrows). Bar = 25 μm.

upper haustorium.

Elongation of Epidermal Cells and Osmiophilic Particles

As the upper haustorium in the parasite stem matured, the haustorial epidermal cells gradually elongated toward the host. In addition, the epidermal cell walls invaginated at the apical ends and produced branches or projections. Lee and Lee (1989) do not mention such a modification; however, those epidermal cells of *C. australis* touching the host are visible in their light micrographs. The differentiation of the epidermal cells into elongated secretory trichomes with invaginated cell walls has been described in other species as well, including *C. reflexa* (Heide-Jørgensen, 1987, 1991b), *Viscum minimum* (Heide-Jørgensen, 1989), *Cassytha pubescens* (Heide-Jørgensen, 1991a), and *Cuscuta pentagona* (Vaughn, 2002).

The cytoplasm in the tip regions of the epidermal cells contained numerous dictyosomes, dictyosome-derived secretory vesicles, r-ER, and polysomes. This reflected the protein biosynthesis and secretion that occurred in the apical ends. Osmiophilic particles within the secretory vesicles were released into the cell walls just outside the plasma membrane. These vesicles are derived from dictyosomes (Hoffmann-Benning et al., 1994; Vaughn, 2002). Previously, osmiophilic particles have been detected where rapid elongation growth occurs, e.g., in many plant tissues (Olsen, 1980), maize coleoptiles and rice internodes (Schopfer, 1990; Hoffmann-Benning et al., 1994; Edelmann et al., 1995), rye coleoptiles (Edelmann and Sievers, 1995; Robinson, 1995; Edelmann and Volkmann, 1996), and the hypocotyls and epicotyls of some angiosperms and gymnosperms

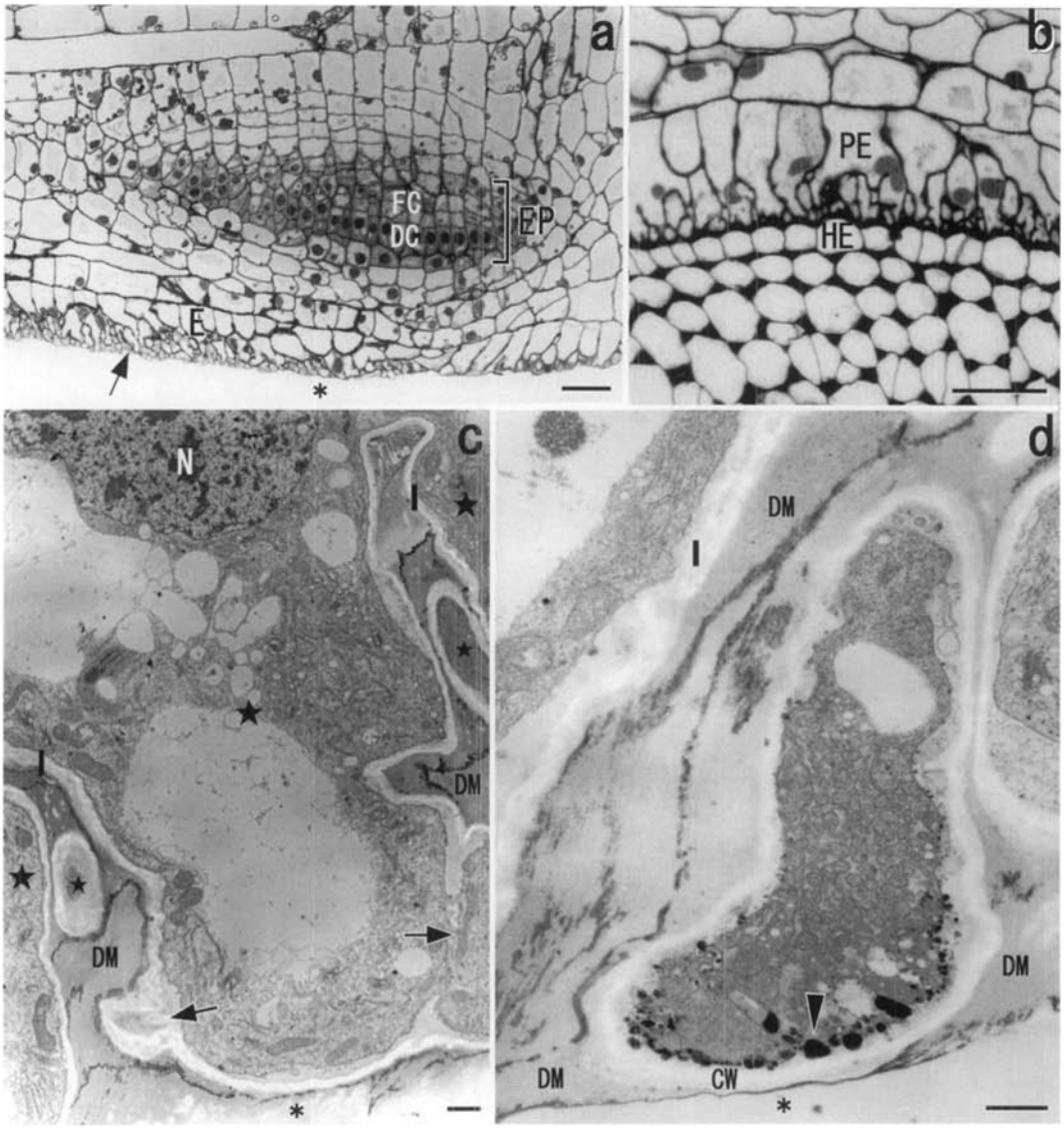

Figure 3. Light (**a-b**) and electron micrographs (**c-d**) showing highly branched epidermal cells. (**a**) Longitudinal section of mature upper haustorium with endophyte primordium (EP) consisting of file cells (FC) and digitate cells (DC). Tips of epidermal cells (E) have numerous projections (arrow). Asterisk(*) indicates sites of host contact. Bar = 50 μm. (**b**) Enlarged view of interface between parasite and host shows tips of epidermal cells (PE) bearing numerous projections. HE, host epidermis. Bar = 25 μm. (**c-d**) Asterisks (*) indicate site of host contact. (**c**) Spaces formed by cell wall invaginations (I) produce toe-like projections (large stars), which branch further (arrows) and make smaller projections (small stars). Projections interlock with each other in spaces. Cytoplasm has nucleus (N) and abundant other organelles. Note accumulation of somewhat dense and homogeneous materials (DM) in spaces between projections. Bar = 1 μm. (**d**) Magnified view of smaller projection containing numerous osmiophilic or electron-dense particles (arrowheads) in cytoplasm and cell wall (CW). DM, dense and homogeneous materials; I, invagination of wall. Bar = 1 μm.

(Samajova et al., 1998). These particles are at least partially proteinaceous (Hoffmann-Benning et al., 1994), and contain the protein expansin (Vaughn et al., 2001). The trichomes of *C. pentagona* shoots that contact the host release osmiophilic particles (components of cell wall-loosening complexes) into the cell walls, allowing them to soften and then elongate and invaginate (Vaughn, 2002). However, the particles detected here in the *C. japonica–Impatiens balsamina* system differed in size and density from components of the cell wall-loosening complex in the system of *C. pentagona–Impatiens sultanii* (Vaughn, 2002). In addition, those complexes reported in the latter parasitic system were not found in this current study.

O'Malley and Lynn (2000) have reported that expansin genes in the root parasite *Striga* are activated when the epidermal cells of the root elongate rapidly and are attached to the host surface. For the *C. japonica* epidermal cells described here, osmiophilic particles were more numerous in each cell than what was found in rapidly elongating maize coleoptiles (Hoffmann-Benning et al., 1994) or elongating pea and bean tissues (Edelmann et al., 1995; Samajova et al., 1998). Vaughn (2002) also has noted a similar relative abundance of particles in the epidermal cells of *C. pentagona*. These osmiophilic particles are associated with the loosening and rapid elongation of epidermal cell walls (Edelmann et al., 1995; Samajova et al., 1998), and

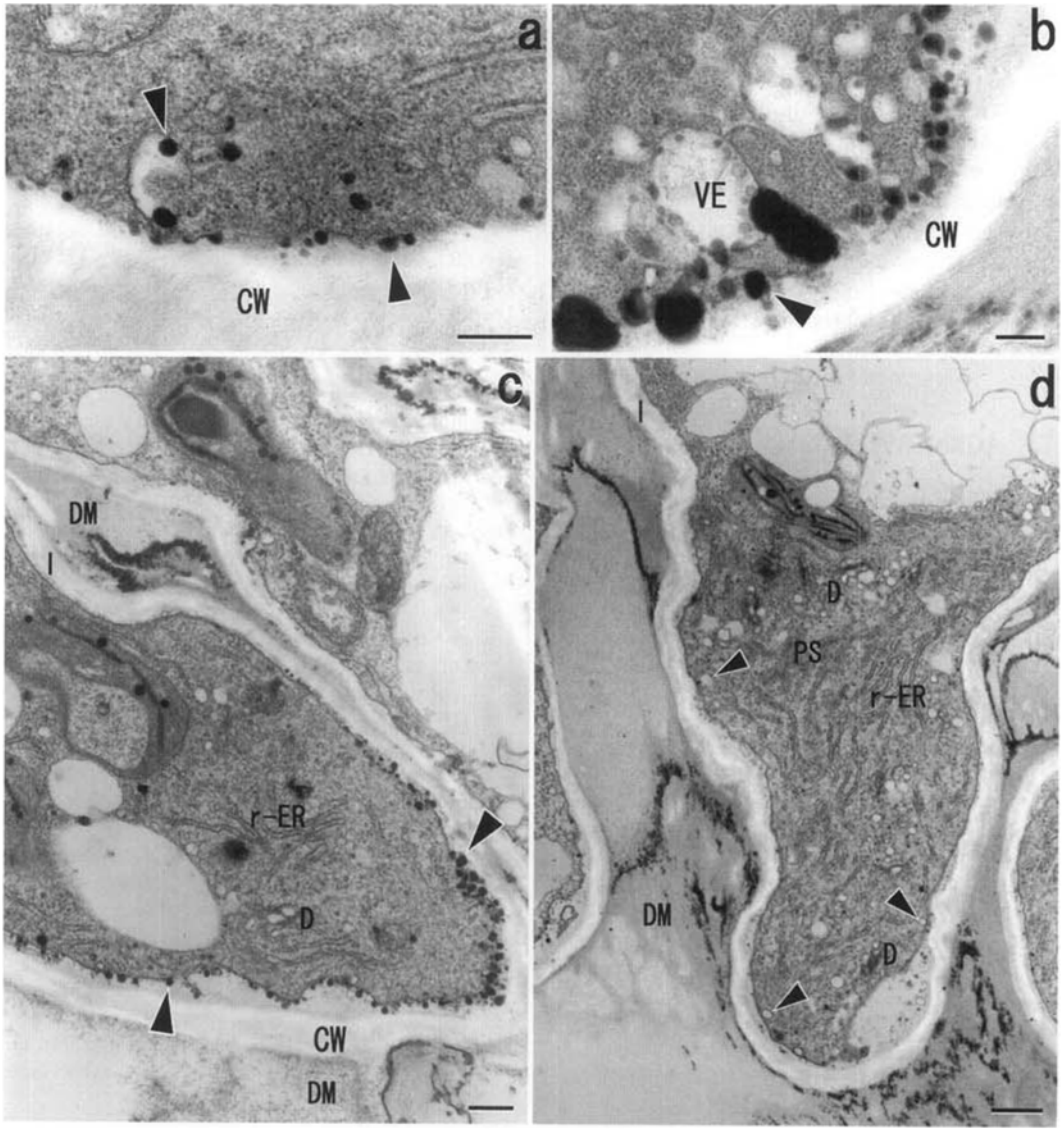

Figure 4. Electron micrographs of branched tip regions of epidermal cells. (**a**) Magnified view showing osmiophilic granules (arrowheads) in vesicle and in cell wall (CW) just outside plasma membrane. Bar = 0.25 μm. (**b**) Enlarged view of vesicles (VE) containing particles in cytoplasm, and osmiophilic osmiophilic particles (arrowhead) in cell wall (CW) just outside plasma membrane. Bar = 0.5 μm. (**c**) Apical region of epidermal cell containing abundant dictyosomes (D) and rough endoplasmic reticulum (r-ER). Electron-dense osmiophilic particles (arrowheads) are along cell wall (CW) just below plasma membrane. DM, dense and homogeneous materials; I, wall invagination. Bar = 0.5 μm. (**d**) Cytoplasm at tip of epidermal cell contains numerous dictyosomes (D), dictyosome-derived vesicles (arrowheads), r-ER, and polysomes (PS). DM, dense and homogeneous materials; I, wall invagination. Bar = 1 μm.

the occurrence of particles is related to the elongation rate (Samajova et al., 1998). Therefore, based on those studies, the loosening and elongation of walls in the *Cuscuta* epidermal cells would perhaps be much greater than in the previously investigated autotrophic plants.

Invagination of Cell Walls

Invagination of the cell walls, followed by elongation of the epidermal cells, caused many toe-like projections to form in the upper haustorium of *C. japonica*. That is, the surface area of the plasma membrane increased and spaces developed between those projections. Slightly dense material accumulated in the spaces between the projections and at the parasite-host interfaces (see Figs. 3c-d, 4c-d). However, the chemical nature of that dense material was not identified in this study. These cell wall invaginations might play an important role in creating the spaces in which adhesive material is deposited. For example, the epidermal trichomes secrete polysaccharide material in *Cuscuta reflexa* (Heide-Jorgensen, 1987), cutinaceous materials in *Viscum minimum* (Heide-Jørgensen, 1989) and *Cassytha pubescens* (Heide-Jørgensen, 1991a), and pectinaceous cement material in *Cuscuta pentagona* (Vaughn, 2002).

In summary, while the *C. japonica* upper haustorium matured, the epidermal cells elongated and their cell walls enfolded to create a firm contact with the host plant. Cell wall invaginations, followed by cell elongation, increased the surface area of the plasma membrane, concurrently producing many toe-like projections and crevices between the

projections. The apical ends of the projections contained a dense cytoplasm with prominent nuclei and other abundant organelles, indicating of protein biosynthesis and secretion. Osmiophilic particles were released from the cytoplasm into the cell walls just outside the plasma membrane. These particles are believed to participate in the loosening and elongating of the epidermal cell walls. Dense materials were secreted into the spaces between projections at the tips of the epidermal cells. This structural transformation of the epidermal cells may facilitate the secretion of a cementing material that could be used by the haustorium to secure a tight attachment to the host surface.

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