New Phytol. (1988), **108**, 229–257

Tansley Review No. 14
Secretory tissues in vascular plants

By ABRAHAM FAHN

Department of Botany, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

(*Received 14 September 1987; accepted 7 November 1987*)

CONTENTS

SUMMARY

Secretory tissues occur in most vascular plants. Some of these tissues, such as hydathodes, salt glands and nectaries, secrete unmodified or only slightly modified substances supplied directly or indirectly by the vascular tissues. Other tissues secreting, for instance, polysaccharides, proteins and lipophilic material, produce these substances in their cells. The cells of secretory tissues usually contain numerous mitochondria. The frequency of other cell organelles varies according to the material secreted. In most glandular trichomes the side wall of the lowest stalk cell is completely cutinized. This prevents the secreted material from flowing back into the plant.

The salt glands in *Atriplex* eliminate salt into the central vacuole of the bladder cell but, in other plants, the glands secrete salt to the outside. Different views exist as to the manner in which salt is eliminated from the cytoplasm. According to some authors, the mode of elimination is an eccrine one, while others suggest the involvement of membrane-bound vesicles.

Nectar is of phloem origin. The pre-nectar moves to the secretory cells through numerous plasmodesmata present in the nectariferous tissue. Nectar is eliminated from the secretory cells by vesicles of either ER or dictyosomal origin. In some cases, both organelles may be involved but an eccrine mode of nectar secretion has also been suggested by some authors.

Carbohydrate mucilages and gums are synthesized by dictyosomes but virtually every cell compartment has been suggested as having a role on the secretion of lipophilic substances. Most commonly, plastids are implicated in the synthesis of lipophilic materials but ER may also play a part. In some cases lipophilic materials may be transported towards the plasmalemma in the ER.

Resin and gum ducts of some plants develop normally or in response to external stimuli, such as microorganisms or growth substances. Among the latter, ethylene is the most effective.

During the course of evolution, secretory tissues seem to have developed from secretory idioblasts scattered among the cells of the ordinary tissues. Subsequently ducts and cavities developed and finally secretory trichomes.

Key words: Secretory tissues, anatomy, ultrastructure, glands, salts, nectar, resin, gum, mucilage.

I. INTRODUCTION

Many of the important natural chemicals, which have been used by man through the ages, are produced by the secretory tissues of vascular plants. These chemicals have various functions in the plants themselves. Some of the secreted substances serve to attract pollinators and vectors in seed dispersal; others deter phytophagous animals. Hydathodes, which secrete water in liquid form, and salt glands are important in plants growing in particular environments. The secreted materials, after being eliminated from the secretory structures, do not usually re-enter the metabolic processes of the plant.

Secretory tissues occur in most vascular plants. They differ in structure, topographic position and in the materials secreted. Some of the secretory tissues (hydathodes, salt glands and nectaries) eliminate unmodified or only slighly modified substances supplied directly or indirectly by the vascular tissues. Others synthesize the secreted substance (e.g. mucilage-, oil- or resin-producing tissues). The secreted material is usually eliminated from the secretory cells to the outside of the plant or into specialized intercellular spaces. In certain cases, as for instance in the laticifers, the secreted material (latex) remains inside the secretory cells.

The secretory tissues may consist of single cells or small to very large groups of cells. Hydathodes, salt-secreting glands, nectaries, stinging hairs and the secretory glands of carnivorous plants lie on the plant surface. Tissues secreting lipophilic substances, gums and mucilages may be present either on the plant surface, mostly in the form of trichomes, or inside the plant body. In the latter case they may be represented by single specialized cells, or by rows of cells (e.g. laticifers), or by structures consisting of an epithelium surrounding an intercellular space. The latter structure, if it is more or less isodiametric in shape, is termed a *secretory cavity*, and when elongated it is called a *secretory duct*.

Secretory tissues are usually classified according to the substances they produce. The various kinds are: hydathodes; salt glands; nectaries; mucilage-secreting cells, trichomes, ducts and cavities; gum ducts; enzyme-secreting glands of carnivorous plants; myrosin cells; stinging trichomes; oil cells; oil-secreting trichomes; osmophores; oil cavities; resin ducts; flavonoid-secreting tissues and laticifers (Fahn, 1979*a*). The same tissue often secretes a number of different substances. The study of the large spectrum of secretory substances and their production by a range of structures, differing greatly in their morphology and anatomy, requires a variety of approaches.

The period of intense research interest in secretory tissues towards the end of the nineteenth and the early part of the twentieth century was marked by numerous publications on subjects ranging from their anatomy and morphology to their usefulness in systematics, the nature of the secretory products and their economic value to physiology in relation to ecology (Bonnier, 1879; Haberlandt, 1886, 1894; Tschirch, 1889, 1906; Müller, 1866–7; Zimmermann, 1932; Frey-Wyssling, 1935; Sperlich, 1939; Kisser, 1958). More recently, secretory tissues have also figured in considerations of the co-evolution of plants and animals (Levin, 1973; Baker & Baker, 1975; Bentley, 1976; Cruden, Hermann & Peterson, 1983). However, the majority of studies over the last 30 years have been biochemical or ultrastructural (see reviews by Metcalfe, 1967; Thurston & Lersten, 1969; Thomson, 1975; Hill & Hill, 1976; Lüttge & Schnepf, 1976 and books by Schnepf, 1969*a*; Vassilyev, 1977; Fahn, 1979*a*).

In this review, selected examples will be used to illustrate phenomena common to a wide range of secretory tissues. Particular emphasis will be placed on the following three aspects: (1) correlations between ultrastructure and the process of secretion; (2) factors influencing the development of secretory tissues; and (3) possible evolutionary trends in the development of secretory tissues.

The cells of the secretory tissues are usually characterized by small vacuoles and relatively dense cytoplasm containing numerous mitochondria. The frequency of other cell compartments and organelles varies according to the particular compound secreted.

A general characteristic, common to almost all secretory trichomes, is complete cutinization of the side walls of stalk cells, similar to that occurring in the walls of the cells of the root endodermis. The presence of these 'endodermal' cells in secretory trichomes indicates that the flow of the secretory substances or their precursors into the trichome takes place exclusively through the symplast and that flow of the secreted substances back into the plant through the apoplast is prevented.

The views on the manner of secretion by the secretory tissues are based largely on the study of ultrastructural changes which occur during the development of the secretory cells. In addition to conventional electron microscopy, cytochemistry, autoradiography and sometimes stereological methods have been applied.

A secretory tissue may consist of cells which are all involved in the elimination of the secreted substance directly into the extracellular milieu (secretory cells), or of such cells together with auxiliary cells that do not secrete directly into the extracellular spaces. In nectaries secreting through stomata for example, all the cells of the nectariferous tissue release the nectar into the intercellular spaces whereas, in nectaries which release

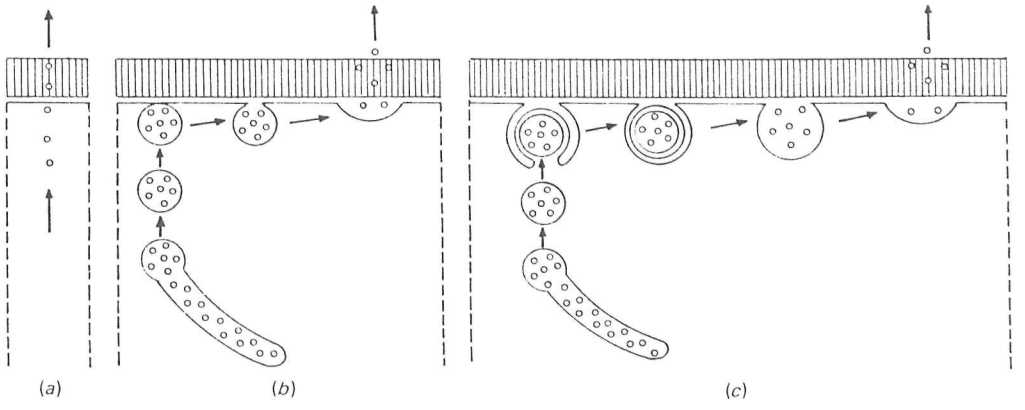

Figure 1. Diagram showing different pathways of secretion from secretory cells in vascular plants. (*a*) Membrane transport – *eccrine secretion*. (*b*, *c*) *Granulocrine secretion*. (*b*) The membrane of a vesicle fuses with the plasmalemma. (*c*) Vesicle elimination is associated with invagination of the plasmalemma. (From Fahn, 1979*a*.)

the nectar to the outside of the plant from epidermal cells or trichomes, the nectariferous cells below the secretory cells transfer the pre-nectar into the secetory cells.

The elimination of the secretory material from the cytoplasm may be carried out in two ways (Fig. 1). The secreted substance passes the plasmalemma (or tonoplast) by an active moleular process-*eccrine secretion*; 2. The secreted substance is collected in membrane-bound vesicles-*granulocrine secretion*. The membranes of the vesicles fuse with the plasmalemma (or tonoplast), or the vesicles containing the secretory material are eliminated from the cytoplasm by invaginations of the plasmalemma, which surround and detach them from the protoplast.

II. SALT GLANDS

1. *Introduction*

Salt glands are specialized epidermal cells or trichomes, which play an active part in the secretion of solutions of mineral salts and often also contain organic substances. Haberlandt (1918) called these 'epidermal hydathodes' or 'active hydathodes', to distinguish them from the hydathodes proper, which he called 'passive hydathodes'. Other authors failed to make such distinctions and used the general terms hydathode or trichome hydathodes and, in specific cases, chalk glands. Ions reported as occurring in the secreted solutions of salt glands are: Na^+, K^+, Mg^{2+}, Ca^{2+}, Cl^-, SO_4^{2-}, NO_3^-, PO_4^{3-} and HCO_3^-. There is no direct connection between the salt glands and the vascular bundles. Salt may be eliminated into vacuoles or to the outside of the glands.

Salt glands occur in several families of dicotyledons and in the Gramineae. In dicotyledons they are characteristic of the Frankeniaceae, Plumbaginaceae and Tamaricaceae, but also occur in some genera of other families, such as Acanthaceae, Chenopodiaceae, Convolvulaceae and Primulaceae. Salt glands are present in many mangrove plants, e.g. *Aegialitis* (Plumbaginaceae), *Aegiceras* (Myrsinaceae), *Avicennia* (Avicenniaceae) and *Laguncularia* (Combretaceae).

2. *Glands eliminating salts into the vacuole*

In *Atriplex* spp., salt is eliminated into a central vacuole of the bladder cell of the leaf trichomes. These cells are situated on top of narrow, 1- to 3-celled stalks. In the early stages of the trichome development the bladder cell lacks vacuoles. Growth of this cell is accompanied by the formation and expansion of a central vacuole (Fig. 2*a*, *b*). At the same time, salt accumulates. Eventually, the bladder cell ruptures, releasing the salt on to the surface of the leaf (Black, 1954). The side walls of the stalk cell or, if the stalk consists of more than one cell, of the lowest cell, become completely cutinized (Fig. 2*a*, *b*) (Osmond *et al.*, 1969; Thomson & Platt-Aloia, 1979).

3. *Glands eliminating salts to the outside of the cells*

Among the glands eliminating salt to the outside of the cells, those of the Gramineae exhibit the simplest anatomy. They consist of two cells, a basal and a cap cell. The position, size and shape of the glands varies between species, (Liphshitz & Waisel, 1974; Liphshitz *et al.*, 1974). The two-celled salt glands of *Spartina*

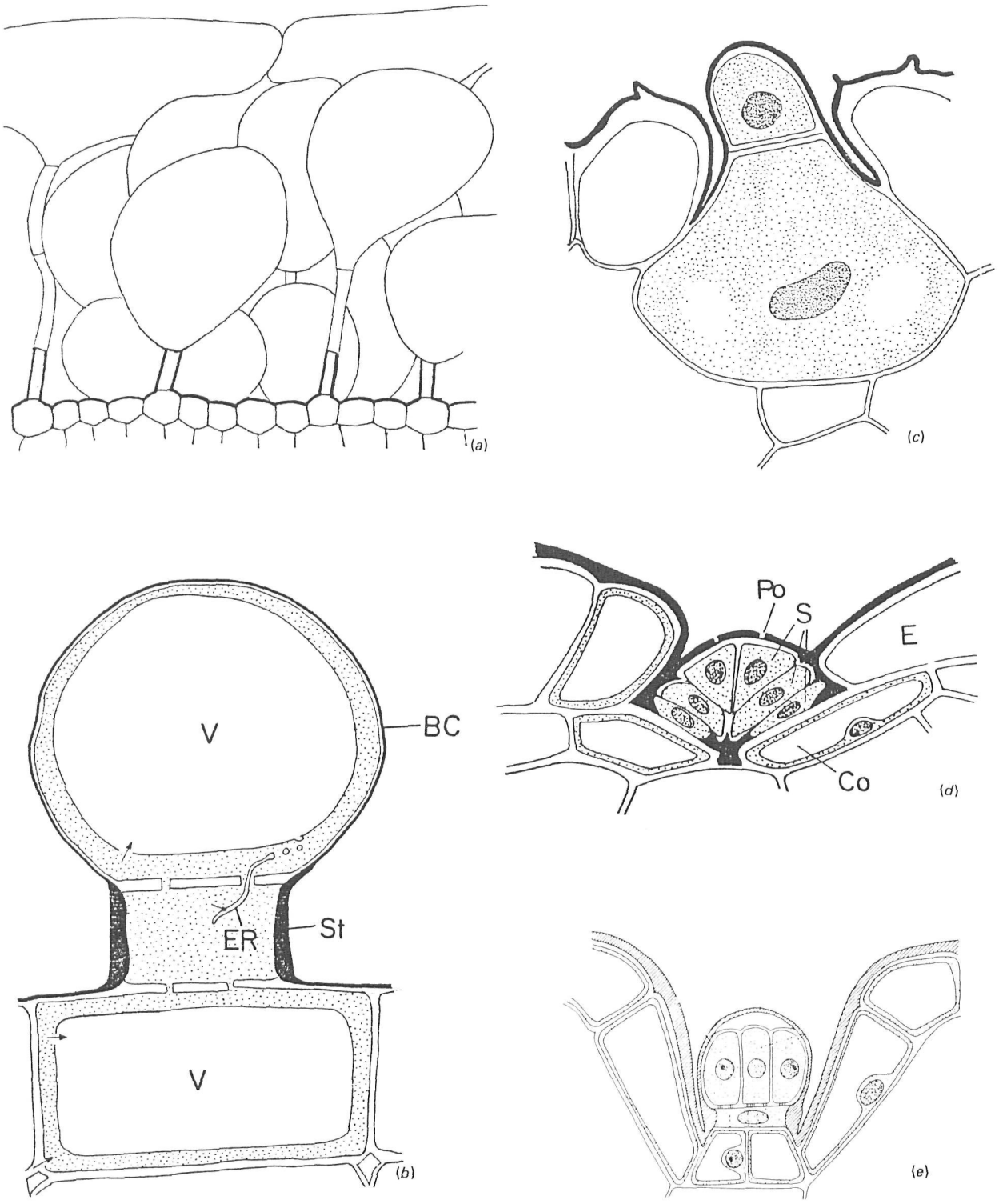

Figure 2. Salt glands. (*a*, *b*) *Atriplex halimus*. L. (*a*) Epidermis and bladder hairs; the lateral walls of the lowest stalk cell are completely cutinized. (*b*) Diagram of a bladder hair, showing possible routes of chloride transfer to the bladder cell and its vacuole. Arrows indicate active transport through membranes. One vesicle is seen fusing with the bladder tonoplast. BC, bladder cell; ER, endoplasmic reticulum; St, stalk cell; V, vacuole. (*c*) *Spartina towsendii*. H. & J. Groves (*d*) *Tamarix aphylla*. Co, collecting cell; E, epidermal cell; Po, pore in the cuticle; S, secretory cell. (*e*) *Avicennia marina*. (*a–d*, from Fahn, 1979*a*; *e*, from Fahn & Shimony, 1977.)

(Fig. 2*c*) possess a cylindrical depression, the 'well', between the cap cell and the four epidermal cells surrounding it (Sutherland and Eastwood, 1916; Skelding & Winterbotham, 1939). A continuous cuticle covers the cap cell, the narrow free upper part of the basal cell and the neighbouring epidermal cells. The cuticle over the upper part of the cap cell is distended and becomes detached from the wall forming a cavity between the two. In the elevated cuticle there are numerous narrow pores filled with electron-dense material. Plasmodesmata occur between the basal cell and the cap cell and between the basal and neighbouring mesophyll cells. However, no plasmodesmata are seen between the basal cell and the four neighbouring epidermal cells. At the top of the basal cell along the thick wall separating the two gland cells, many long wall protuberances extend into the basal cell. The plasmalemma along these protuberances forms very long invaginations extending nearly to the base of the basal cell. The cytoplasm of this cell is dense and particularly rich in mitochondria. It also contains some rough endoplasmic reticulum, dictyosomes, a few plastids, small vesicles and multivesicular structures. The cytoplasm of the cap cell is in general similar to that of the basal cell, except that the plastids are more prominent. In contrast to other salt glands and secretory trichomes in general, cutinization of the side walls of the basal cell is uncomplete in the graminaceous species investigated (Levering & Thomson, 1971). The manner of salt secretion in *Spartina* has yet to be elucidated (Levering & Thomson, 1972; Thomson & Healey, 1984).

The salt glands of *Limonium*, *Tamarix*, *Avicennia* and many other dicotyledonous plants are multicellular (see Fahn, 1979*a*). The salt glands of *Tamarix aphylla* (L.) Karst., whose ultrastructure was studied by Thomson & Liu (1967) and by Shimony & Fahn (1968), consists of 8 cells (Fig. 2*d*). The two-vacuolated basal cells are termed *collecting cells*. The six upper cells with dense cytoplasm are the *secretory cells*. The secretory cells are enclosed by a cuticle except for portions of the walls between the two lowest secretory cells and the collecting cells (Fig. 2*d*). These wall portions which are penetrated by numerous plasmodesmata (Fig. 4*a*), are termed *transfusion areas*. The side walls of the lowest secretory cells are completely cutinized. These walls are lined by a complex extracytoplasmic structure known as the 'intrafacial apparatus'. It contains a variety of vesicles and lamellae (Bosabalidis & Thomson, 1984). In the upper secretory cells, wall protuberances are present. On top of the gland, several distinct pores traverse the cuticle (Fig. 3). Numerous mitochondria and plastids occur in the uppermost pair of the secretory cells. The plastids are electron-dense and contain osmiophilic droplets. Vesicles interconnected by lamellae form several concentric series in the peripheral region of the plastids. Along the walls and their protuberances, there are many vesicles and small vacuoles containing electron-dense material (Fig. 3). Multivesicular structures are also visible in the cytoplasm. Ribosomes and polysomes are more abundant in secretory cells of plants grown in high NaCl concentration than those grown in low concentrations of NaCl. The protoplasts of the collecting cells resemble those of the mesophyll cells. Electron-dense material, apparently of a pectic nature, occurs above the cuticle on top of the gland, between this portion of the cuticle and the cell walls and in the cuticular pores (Fig. 3). This material forms a continuous channel system with the cell walls and their protuberances, and would appear to be the route by which the secreted salt solution reaches the outside of the plant.

The salt gland of the mangrove *Avicennia* (Fig. 2*e*) consists of 2–4 collecting cells, one disc-like stalk cell and usually eight, but sometimes up to 12, radially arranged secretory cells (Walter & Steiner, 1937; Chapman, 1944). The electron microscopical study carried out by Shimony, Fahn & Reinhold (1973) on the salt glands of *Avicennia marina* (Forssk.) Vierh., revealed many similarities between their ultrastructure and that of the glands of *Tamarix* (Fig. 4*b–d*). At the top of the gland, the cuticle is traversed by pores, which are here numerous and very narrow (Fig. 4*b*). The side walls of the stalk cell are completely cutinized and the cytoplasm adheres strongly to them (Fig. 4*d*). The transverse walls of this cell contain numerous plasmodesmata. Between the cuticle and the upper walls of the secretory cells, moderately electron-dense homogeneous material, probably of a pectic nature, is present. It is often also seen on the inner surface of the side walls of the secretory cells (Fig. 4*c*). It may function as a flow channel for the secreted salt solution in the same manner as the electron-dense material of the glands of *Tamarix*. Inside the secretory cells, the cytoplasm occupies most of the cell volume. The nucleus is large and mitochondria and ribosomes numerous. Vesicles (Fig. 4*c*), some with dense contents, frequently form aggregation in the peripheral cytoplasm. Multivesicular structures often occur between the plasmalemma and the cell wall.

4. *Structure and function*

Lüttge (1969, 1971) reviewed the hypotheses about the uptake of ions from the xylem and their translocation through the mesophyll to the salt glands. According to Shimony *et al.* (1973), a downhill salt gradient appears to exist in leaves of *Avicennia* from near the xylem to the gland, and is continued through the gland itself, the secretory cells having the lowest salt content. Thomson (1975), Campbell & Thomson (1976*a*, *b*) and Van Steveninck *et al.* (1976) discussed the question of apoplastic versus symplastic transport of salt to the gland. However, this problem has not yet been resolved.

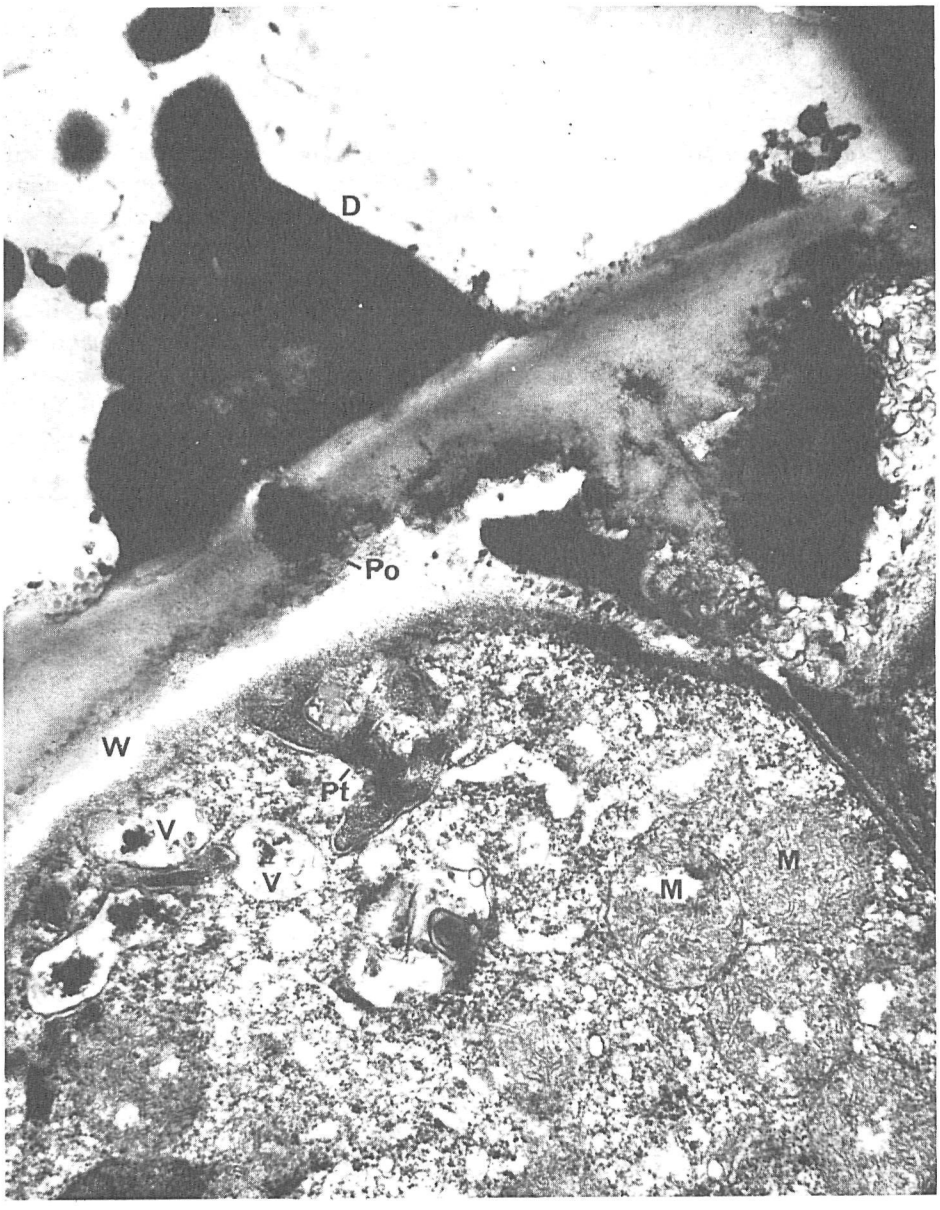

Figure 3. Upper part of a salt gland in *Tamarix aphylla*; D, electron-dense pectic material; M, mitochondrion; Po, pore in the cuticle, filled with electron-dense material; Pt, wall protuberance; V, vesicles; W, cell wall. ×23000. (From Shimony & Fahn, 1968.)

As already mentioned, the cytoplasm of the secretory cells of salt glands is rich in ribosomes and contains a large nucleus and numerous organelles, particularly mitochondria. This supports the view that the elimination of ions from the cytoplasm requires energy.

The basic question of how the salt solution is eliminated from the cytoplasm of the secretory cells has yet to receive a definite answer. As numerous vesicles and small vacuoles occur in the secretory cells, many in the peripheral cytoplasm, several authors have suggested that they are involved in the process of secretion (Thomson & Liu, 1967; Shimony & Fahn, 1968; Osmond *et al.*, 1969; Thomson, Bery & Liu, 1969; Shimony *et al.*, 1973). Thomson & Healey (1984) hypothesized that the primary mechanism involved in the transport of salt across membranes into the vacuole of *Atriplex*, into the outer spaces of the plasmalemmal invaginations in graminaceous glands and into the vesicles and/or across the plasmalemma of the secretory cells of multicellular glands, is an eccrine process.

The transport of the salt solution, after it has been eliminated from the protoplasts of the two-celled and the multicellular glands, takes place in the wall. The cell wall of the secretory cells seems to be particularly adapted for this purpose. In many cases (e.g. *Tamarix*, *Spartina*) wall protuberances extend into the cell. The wall protuberances and to some extent the wall itself, appear to be rich in pectic substances, thus having

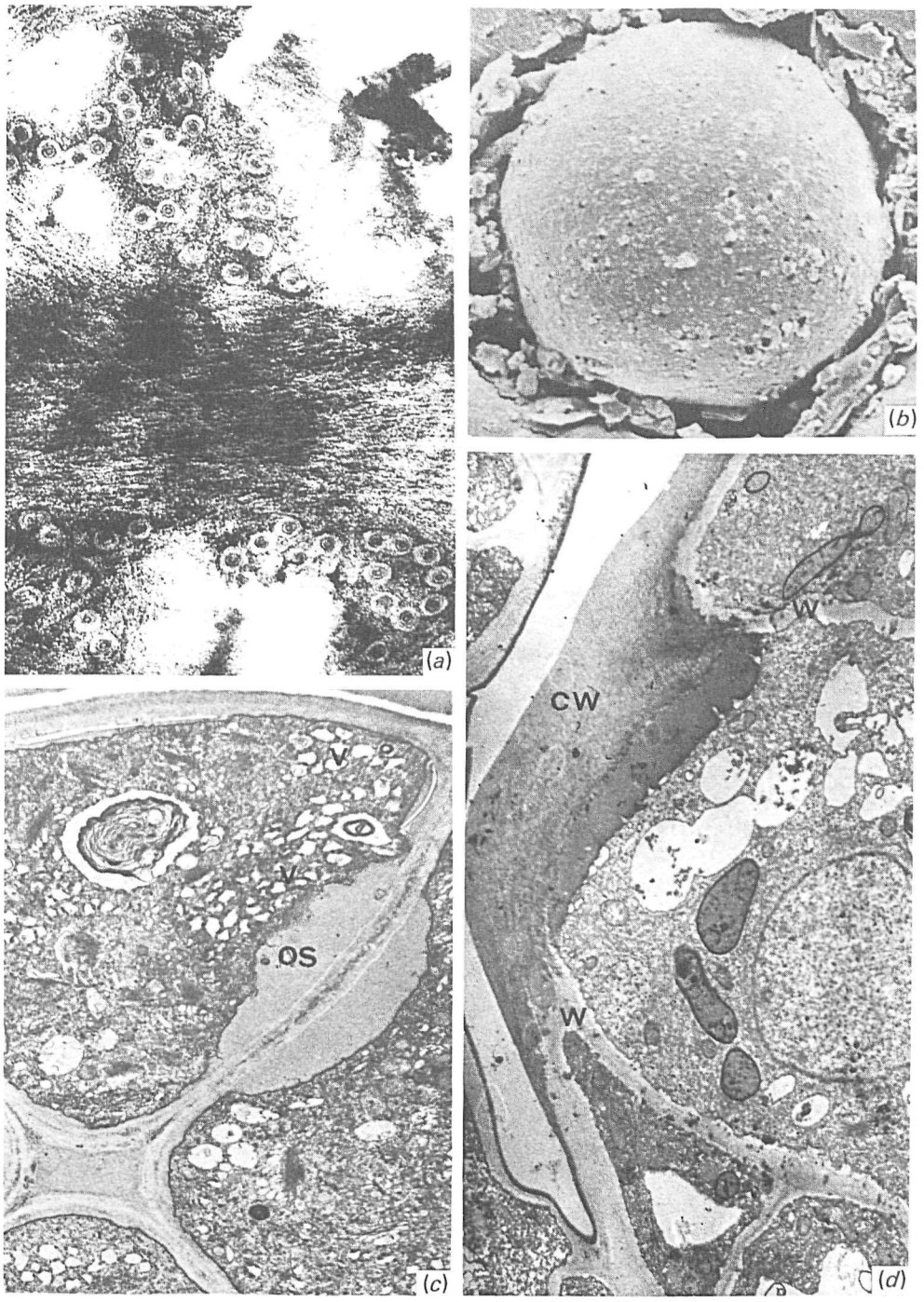

Figure 4. Salt glands. (*a*) Tangential section of the wall between a collecting cell and a neighbouring secretory cell of a gland in *Tamarix aphylla*, showing numerous plasmodesmata ×50000. (*b–d*) *Avicennia marina*. (*b*) Scanning electron micrograph of a gland. Many minute pores are visible in the cuticle. ×11000. (*c*) cross-section of a young gland, showing numerous vesicles (V) and an opaque substance (OS) (apparently of a pectic nature) between the protoplast and the cell wall. ×7000. (*d*) Longitudinal section showing the completely cutinized side wall (CW) of the stalk cell; W, cutin-free cell wall. (From Fahn, 1979*a* and Shimony *et al.* 1973.)

favourable properties for the absorption of solutions. In addition, protuberances which are lined by the plasmalemma greatly enlarge the surface of the protoplast as in many other cells in which short-distance transport takes place. Such transfer cell morphology (Pate & Gunning 1972) would clearly appear to facilitate the transport of solutes between the symplast and its extracellular environment. The back flow of the secreted salt solution through the apoplast into the neighbouring tissues is blocked, at least in the dicotyledons, by the endodermal cells (Schrodter, 1926; Schnepf, 1969*a*; Fahn, 1979*a*).

III. NECTARIES

1. *Introduction*

Caspary (1848) distinguished between *floral* and *extrafloral nectaries*; the former occurring in flowers, the latter on vegetative organs. Delpino (1868-75), who considered the function of the nectaries, proposed the terms *nuptial* and *extranuptial nectaries*; the first for nectaries occurring within the flower, which are directly associated with pollination, and the second for nectaries occurring on the outside of the outer floral parts and on vegetative organs, which are not directly associated with pollination. The terms floral and extrafloral nectaries are now commonly used in the same sense as Delpino used the terms nuptial and extranuptial nectaries (Elias & Gelband, 1976; Fahn, 1979a, b).

Delpino (1868–75) expressed the view that the extrafloral nectaries of all plants function in attracting ants that defend the plants against herbivores. Darwin (1876) doubted whether in all cases the extrafloral nectaries serve this purpose. He mentioned, for instance, that *Pteridium aquilinum* (l.) Kuhn is very rarely attacked and yet, as discovered by his son Francis, at the base of the fronds there are large nectary glands. However, Darwin agreed that in some cases, such as in *Passiflora* and *Acacia*, secretion by the extrafloral nectaries 'serve to attract insects as defenders of the plant'. Recently, much attention has been paid to the function of the extrafloral nectaries, and more and more evidence has been obtained in support of the view that they attract ants, which protect the plants bearing them from damage by herbivores (Bentley, 1977; Schemske, 1980; Keeler & Kaul, 1984).

2. *The structure of nectaries*

Nectaries occur on plant surfaces. They may be either flush with the surface of the plant or may form outgrowths or be sunken, in some cases very deeply, as for instance are the septal nectaries of many monocotyledons. The nectary consists of a modified epidermis, with or without trichomes, and specialized parenchyma. The tissue which constitutes the nectary is called *nectariferous tissue*. The cells of this tissue, especially of the parenchyma, are usually small and contain a dense granular cytoplasm and a relatively large nucleus (Caspary, 1848; Behrens, 1879; Bonnier, 1879; Fahn, 1952). The nectaries either abut the ordinary vascular bundles of the organs on which they occur, or contain special bundles, which are connected with the ordinary vasculature. The special vascular bundles may consist of both phloem and xylem or of phloem alone (Frei, 1955; Kartashova, 1965; Fahn, 1979*a*; Said, 1982; Davis, Peterson & Shuel, 1986; Dafni, Lenski & Fahn, in preparation). Nectar is exuded from the nectary either from the epidermal cells or by trichomes or by the nectariferous parenchymatous cells. In the latter case, the cells secrete the nectar into the intercellular spaces, whence it moves to the outside of the nectary either via modified stomata or via lysigenous cavities, as for instance in the extrafloral nectaries of *Sambucus* (Fahn, 1987*a*) (Fig. 5*a–c*).

3. *Nectar and its source*

Secreted nectar consists mainly of sugars but with small amounts of other substances. The most common sugars are sucrose, glucose and fructose, with smaller amounts of maltose, raffinose, galactose and melibiose. Based on quantitative relationships between sucrose and glucose–fructose, three main types of nectar have been distinguished: (1) sucrose-dominant; (2) glucose–fructose dominant; (3) those with an equal ratio of sucrose:glucose–fructose (Fahn, 1949; Percival, 1961; Bahadur, Chaturvedi & Swamy, 1986). The ratio between the different sugars is generally constant within a species but may differ markedly between species, sometimes even between closely related ones (Baker & Baker, 1983*a*, *b*). The other substances reported in nectar are polysaccharidic mucilage, proteins (mainly enzymes, among them transglucosidase and transfructosidase), amino acids, lipids, organic acids, ascorbic acid (functioning apparently as an antioxidant) mineral ions, phosphates and alkaloids (Lüttge; 1961; Baker & Baker, 1975, 1983*a*, *b*; Fahn, 1979*a*). Baker & Baker (1973*a*, *b*) found amino acids in a minor but significant amount in 260 of 266 plant nectars examined. These authors concluded that the amino acids significantly affect the flower-visiting behaviour of potential pollinators. Butterfly-pollinated flowers, for instance, appear to produce nectar containing high concentrations of amino acids more consistently than bee flowers. This difference may be related to the fact that bees have an alternative source of amino acids in pollen.

The origin of the secreted nectar is the phloem sap (Frey-Wyssling & Agthe 1950; Zimmermann, 1953; Frey-Wyssling, 1955; Matile, 1956). The pre-nectar moves from the sieve elements to the cells of the nectariferous tissue. In the nectariferous tissue the pre-nectar may become modified by enzymic activity and by the process of reabsorption (Ziegler & Lüttge, 1959; Lüttge, 1961; Shuel, 1961; Ziegler, 1965). The changes occurring in the pre-nectar of extrafloral nectaries of *Ricinus communis* L. are recorded by Baker, Hall & Throp (1978).

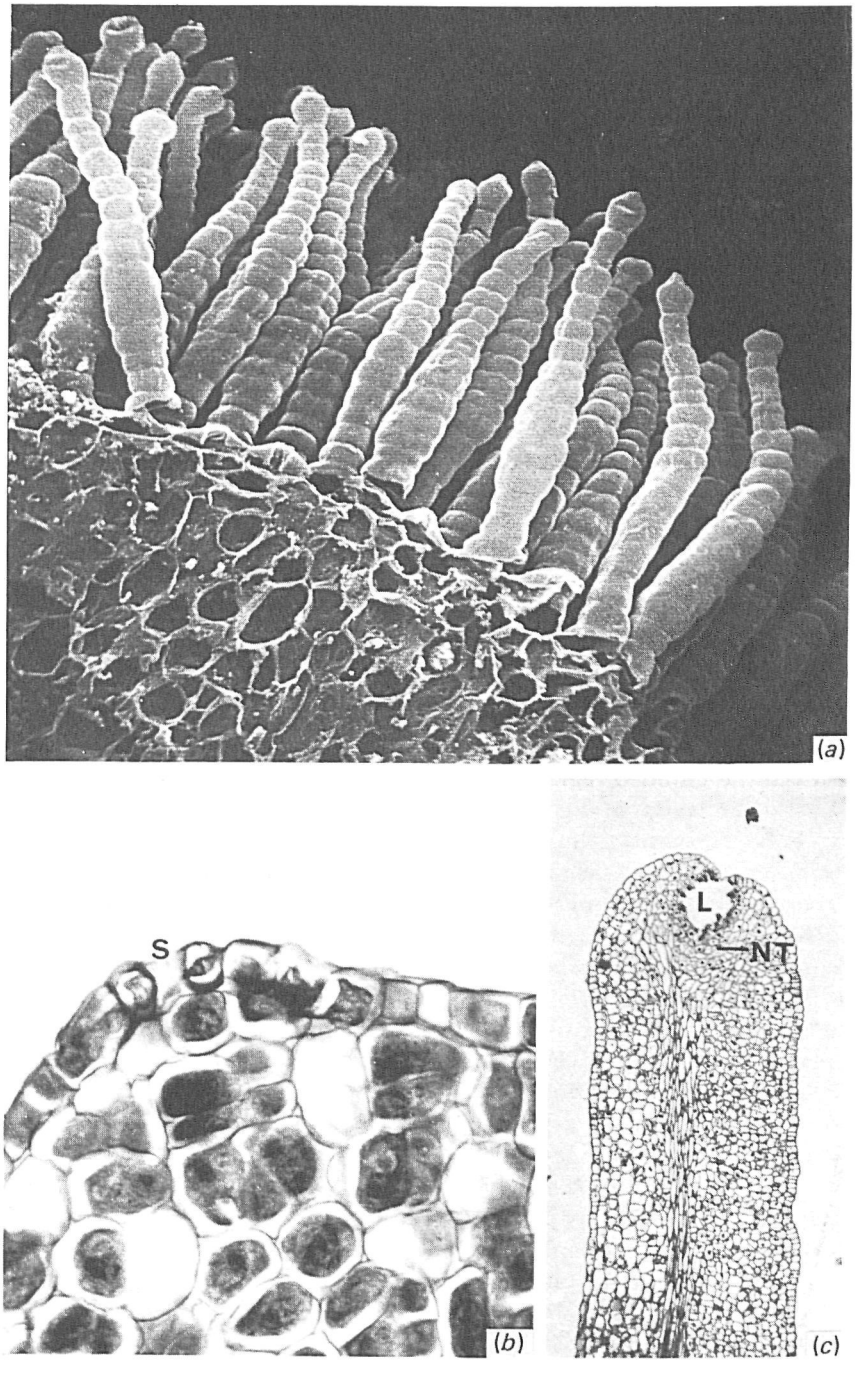

Figure 5. Nectaries. (*a*, *b*) Floral nectaries. (*a*) *Abutilon pictum* Walp. Rep., scanning electron micrograph. × 300. (*b*) *Vinca major* L.; S, stoma. × 500. (*c*) Extrafloral nectary of *Sambucus nigra* L.; L, lysigenous cavity; NT, nectariferous tissue. × 50.

Bieleski & Redgwell (1980) suggested that there is a bidirectional movement of sugars, from the nectary to the outside and from the secreted nectar back into the nectary. According to these authors the two-way transfer of sugars plays a significant part in the final sugar composition of the nectar.

The factors governing the preferential flow of the pre-nectar towards the secretory cells rather than to neighbouring cells are not yet clear. It has been suggested that hydrolysation of sucrose into its monomers may play a role in forming a sink for sugars in the nectariferous tissue. As a result, a sucrose concentration gradient could be maintained which causes a passive flow of sucrose from the sieve elements to the nectar-secreting cells (see Lüttge & Schnepf, 1976; Lüttge, 1977; Meyberg & Kristen, 1981). However, this cannot be the case in nectaries where sucrose is the dominant sugar secreted. Lüttge (1977) considers an active transmembrane transport to play the main role in sugar movement, but, exocytosis and endocytosis may also

take place. Elimination of the nectar from the secretory cells of the nectary may occur via either eccrine or granulocrine pathways (see later).

4. *The ultrastructure of nectariferous tissue*

The walls of the secretory cells of many plants possess protuberances on their inner surface, which may be developed to different amounts depending on the species. They may be very small and inconspicuous, as in the epithelial cells of the septal nectaries of *Tillandsia* (Cecchi Fiordi & Palandri, 1982); somewhat larger as in the septal nectaries of the banana (Fahn & Benouaiche, 1979); or they may form a thick labyrinthine layer as in the septal nectaries of *Gasteria trigona* Haw. (Schnepf, 1969*a*) in the corolla nectaries of *Lonicera japonica* (Fig, 6*a*, *b*) (Fahn & Rachmilevitz, 1970) and in the secretory trichomes of the extrafloral nectaries of *Vicia faba* L. (Tarkowska, Zobel & Maciak, 1981). In the wall of the apical side of the epithelial cells of the *Cynanchum* nectary, Christ & Schnepf (1985) found channel-like structures of low electron density.

The free surface of the nectary may be covered by a thin or thick cuticle. In nectaries which secrete through papillae or multicellular trichomes, the side walls of the lower part of the papillae or those of the lowest cells of the multicellular trichomes (the stalk cells), are completely cutinized (see Fahn, 1979*a*, *b*). This wall structure and its function, which is characteristic of almost all secretory trichomes, has been previously discussed in the section on salt glands.

The walls of the nectariferous cells contain numerous plasmodesmata (Fahn & Rachmilevitz, 1970; Findlay & Mercer, 1971; Wergin *et al.*, 1975; Zandonella & Piolat, 1982). Eleftheriou & Hall (1983) have observed, in the extrafloral nectaries of cotton, ER cisternae close to or oriented towards the plasmodesmata.

The volume of the cytoplasm in the nectariferous cells is relatively large. With the growth of the cells towards the stage of secretion, the volume of the vacuoles may increase. The cytoplasm is usually dense, and rich in ribosomes. The plasmalemma is often highly convoluted, and in many nectaries multivesicular structures occur between the infolded regions of the plasmalemma and the cell walls (Eymé, 1967; Fahn & Rachmilevitz, 1970; Rachmilevitz & Fahn, 1973; Kalman & Gulyás, 1974; Belin-Depoux & Clair-Muczulajtys, 1975; Fahn & Benouaiche, 1979; Mohan & Inamdar, 1986). In many plants, vesicles occurring in the cytoplasm can also be seen to be in contact with the plasmalemma (Fahn, 1979*b*; Eleftheriou & Hall, 1983). In most nectaries endoplasmic reticulum is highly developed, and its cisternae are often arranged in stacks. The ER is mainly rough, but at the stage of secretion it may become part smooth. At this stage, the ER cisternae are dilated and associated with vesicles (Fig. 6*b*) (Fahn & Rachmilevitz, 1970; Fahn & Beouaiche, 1979; Schnepf & Christ, 1980; Eleftheriou & Hall, 1983; Mohan & Inamdar, 1986). In many nectary cells, in addition to ER, numerous active dictyosomes are present (Eymé, 1966; Figier, 1968; Tacina, 1973; Benner & Schnepf, 1975; Fahn & Benouaiche, 1979; Christ & Schnepf, 1985; Marginson, Sedgley & Knox, 1985*a*; Marginson *et al.*, 1985*b*).

At the stage of secretion the nectary cells contain numerous mitochondria, the cisternae of which are usually well developed (Fahn & Rachmilevitz, 1970; Eriksson, 1977; Schnepf & Christ, 1980; Mohan & Inamdar, 1986). In *Cynanchum vincetoxicum* Pers. Christ & Schnepf (1985) have seen that most of the mitochondria are aggregated into complexes. Plastids occur in varying numbers. They have very few thylakoids, and most contain starch grains. In some plant species, at the stage preceding secretion, the amount of starch is very large (Durkee, Gaal & Reisner, 1981; Durkee, 1982). An increase in the amount of starch grains towards the stage of secretion and its subsequent decline has recently been observed in the nectaries of *Rosmarinus officinalis* (Dafni & Fahn, unpublished results). Free osmiophilic globuli are often present in the cytoplasm.

5. *Ultrastructure and the process of secretion*

(*a*) *Transport of pre-nectar*. Several possible pathways by which the pre-nectar flows from the phloem endings, through the parenchymatous cells of the nectary and into the secretory cells, have been suggested. (1) Via the apoplast (Vassilyev, 1969, 1971; Schnepf & Deichgräber, 1984). (2) Via exocytosis and endocytosis (tentatively suggested by Eymé, 1966, and Findlay & Mercer, 1971); in this pathway multivesicular structures may take part (Kalman & Gulyás, 1974). (3) Molecular transport across the plasmalemma of successive cells and passage through cell walls. (4) Via plasmodesmata.

The first possible pathway can be discarded, at least in the case of nectaries which secrete from trichomes, because of the presence of the endodermal stalk cells. The second pathway would involve repeated secretion and absorption of pre-nectar as it passes from cell to cell through the cell wall.

Many studies lead to the conclusion that the transport of the pre-nectar is mainly in the symplast. Numerous plasmodesmata traverse the walls of nectariferous cells (Fahn & Rachmilevitz, 1970; Findlay &

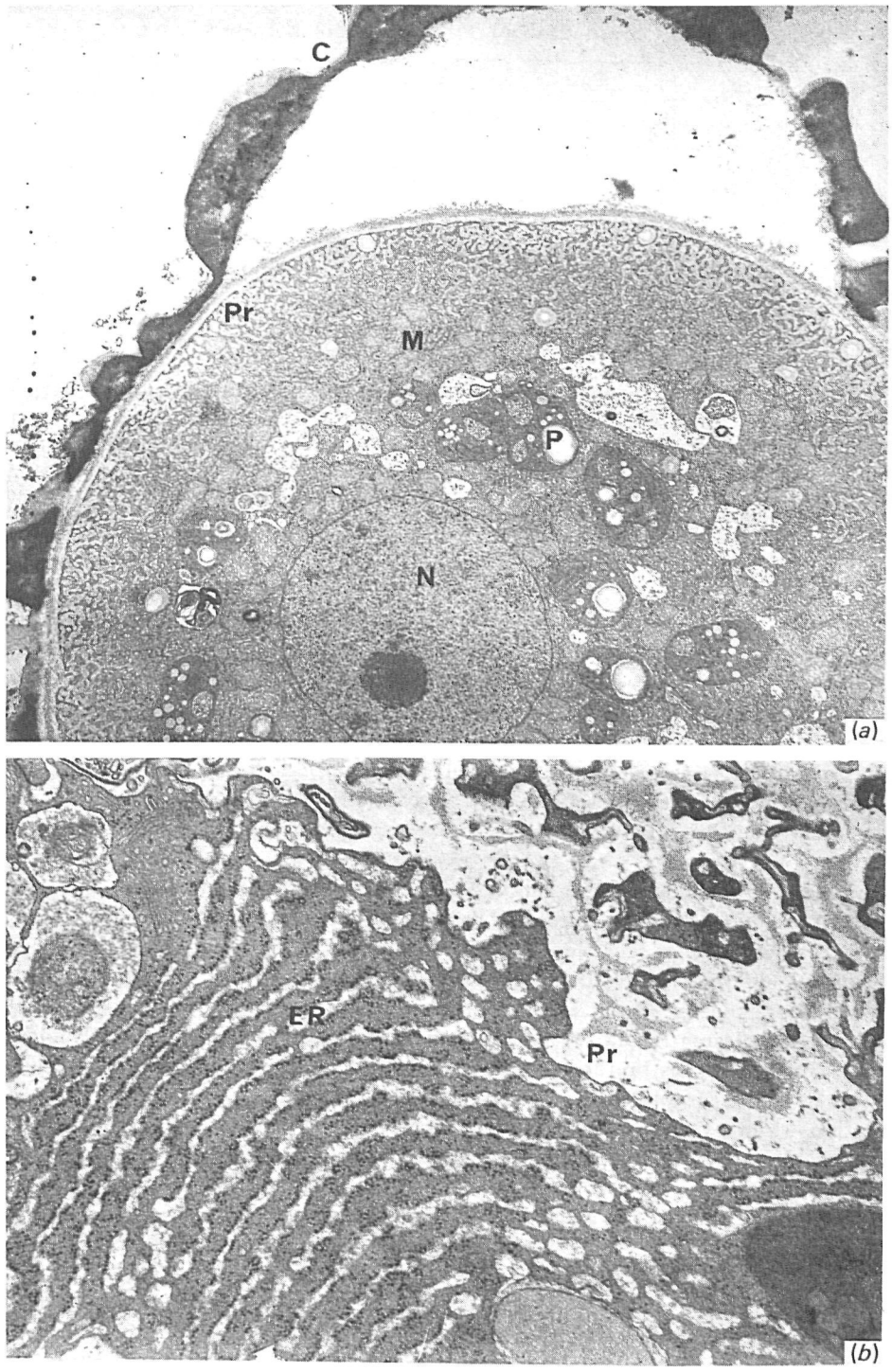

Figure 6. Secretory papillae in the nectary of *Lonicera japonica* Thunb. (*a*) The cuticle (C) is partly detached from the cell wall. The latter possesses a thick layer of wall protuberances (Pr); M, mitochondria; N, nucleus; P, plastids. ×3500. (*b*) At the edges of the parallel sheets of ER cisternae vesicles are present; Pr, wall protuberances. ×16000. (From Fahn & Rachmilevitz, 1970.)

Mercer, 1971; Wergin *et al.*, 1975; Eleftheriou & Hall, 1983; Kronestedt *et al.*, 1986). Gunning & Hughes (1976) studied the nectary trichomes of *Abutilon*, and found a high frequency of plasmodesmata in the periclinal cell walls. These authors have calculated that the required sugar flux through the endodermal stalk cell of the trichome is 3–4 orders of magnitude greater than quoted in the literature for flux through cell membranes. On the other hand the number and dimensions of the plasmodesmata in the distal periclinal wall of the endodermal stalk cell provide a low-resistance pathway for bulk flow of sugar solution. Their study thus supports the view that the pre-nectar flows through the plasmodesmata.

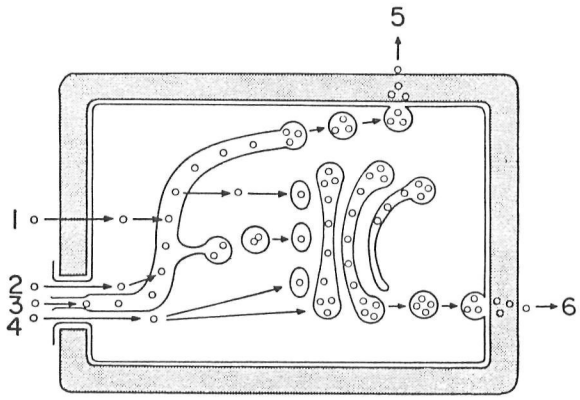

Figure 7. Diagram presenting various possible ways of pre-nectar transport into secretory cells and nectar elimination from them. (1) Molecular transport through the plasmalemma and into the ER; (2) transport through the cytoplasmic annulus of a plasmodesma into the protoplast and the entry into the ER by membrane passage; (3) entry into the ER of the secretory cell through the desmotubule of a plasmodesma; (4) as in (2) but entering a Golgi body; (5) elimination of nectar by fusion with the plasmalemma of vesicles which originated from ER; (6) elimination of nectar by fusion of Golgi vesicles with the plasmalemma. (From Fahn, 1979*a*.)

(*b*) *Transport of nectar outward from the secretory cells.* Two main modes of transport of nectar to the outside of the protoplast of secretory cells have been suggested. There are theories of active molecular transport through membranes – eccrine secretion (see Lüttge & Schnepf, 1976), and of transport via vesicles whose membranes fuse with the plasmalemma – granulocrine secretion (Fig. 7).

In 1964 Schnepf expressed the view that in the septal nectaries of *Gasteria* and some other Liliaceae, nectar transport is a molecular process at the plasmalemma; amplification of the plasmalemma, resulting from the development of wall protuberances, was associated with the onset of nectar secretion. The possibility of molecular transport of sugars within the nectary of *Abutilon* was discussed by Reed, Findlay & Mercer (1971).

Fahn & Rachmilevitz (1970) and Rachmilevitz & Fahn (1973) studied the changes in the ultrastructure of the secretory cells of the nectaries of *Lonicera*, *Vinca* and *Citrus*, at various developmental stages. They observed that, towards the phase of secretion, there is a pronounced increase in the amount of the ER with the cisternae becoming dilated, and associated with numerous vesicles (Fig. 6). In some nectaries ER cisternae lay adjacent to the plasmalemma. On the basis of these observations it was suggested that the vesicle membranes fuse with the plasmalemma. Presumably the nectar accumulates in the ER and is transported to the plasmalemma in the vesicles budded off from its cisternae. The membranes of the two fuse and the nectar is eliminated from the protoplast by reverse pinocytosis. This view has been supported by a number of other investigations (Belin-Depoux & Clair-Maczulajtys, 1975; Eleftheriou & Hall, 1983).

Suggestions that Golgi vesicles rather than vesicles originating from ER origin are involved in outward transport of the nectar have been made by a number of authors (Eymé, 1966; Tacina, 1973; Figier, 1968, 1971; Benner & Schnepf, 1975). In the nectary of the calyx spur of *Tropaeolum majus* L. (Rachmilevitz & Fahn, 1975) and in the septal nectary of *Musa paradisiaca* L. var. *sapientum* (Fahn & Benouaiche, 1979), numerous dictyosomes bud off vesicles at the stage of secretion. Dilated ER cisternae and ER vesicles were also numerous. It was thus suggested that in the nectaries of these plants both the endoplasmic reticulum and the Golgi apparatus are involved in nectar secretion. A similar suggestion was made by researchers who worked on nectaries of some other plants (Marginson *et al.*, 1985*a*; Schnepf & Christ, 1980; Christ & Schnepf, 1985).

The nectaries of some plants, such as those of the banana (Fahn & Benouaiche, 1979), secrete a nectar which contains polysaccharides and protein in addition to sugar. It has been suggested that in these nectaries the secretion of polysaccharides and protein also involves the ER and the Golgi apparatus.

In addition to developmental ultrastructural studies labelling and histochemical techniques have also been applied to secretory cells. Heinrich (1975*a*) studied the localization of phosphatases in the secretory epithelium of the septal nectaries of *Aloë*. He found high activity at ATPase, nucleoside diphosphatase and glucose-6-phosphatase in the ER and generally an absence of activity of these phosphatases in the plasmalemma. Heinrich thus assumed that the endoplasmic reticulum plays an important role in nectar transport. Figier (1972), who tried to localize acid phosphatase in petiolar nectaries of *Impatiens*, also observed only limited reactions on the plasmalemma and the cell walls, except of the sieve tubes and the transfer cells, where he found heavy deposits of the reaction product.

Attempts to follow the path of sugar in the nectary by means of autoradiography were made by Fahn & Rachmilevits (1975) and by Heinrich (1975*b*). After feeding floral nectaries of *Lonicera* with tritiated sucrose the ER and vesicles in the secretory cells became labelled. In the nectariferous tissue below the secretory cells, labelling was frequently observed in the plasmodesmata. Heinrich, on the basis of labelling the septal nectaries of *Aloë* with tritiated glucose, concluded that the nectar is secreted by vesicles, but could not decide whether they originated from ER or from dictyosomes.

IV. MUCILAGES AND GUMS

Mucilages and gums consist principally of polysaccharides although some mucilages also contain proteins. No exact distinction can be made between mucilage and gum, but in general the viscosity of the gums is usually higher than that of the mucilages.

Plant mucilages are complex acid and/or neutral polysaccharide polymers of high molecular weight. They may act as food sources, as an adhesive in seed dispersal, in regulation of seeds germination, in the capture of insects by carnivorous plants, as lubricant of growing root tips and, in root–microorganism interactions (Horner & Lersten, 1968; Gutterman, Witztum & Evenari, 1967; Fahn, 1979*a*; Distelbarth & Kull, 1985; Rougier & Chaboud, 1985).

Mucilages may be secreted by solitary cells (*Hibiscus esculentus* L., *Opuntia ficus-indica* Mill.), by secretory trichomes (*Rumex*, *Psychotria*), or by ducts and cavities (*Sterculia*, *Brachychiton*) (Schnepf, 1968; Lersten, 1975; Metcalfe & Chalk, 1983; Baas & Gregory, 1985). Gum ducts that develop as a result of injury or infection occur in *Liquidambar styraciflua* L., *Acacia* species, members of the Prunoideae and *Citrus* species (Fig. 8*a*, *b*) (Gedalovich & Fahn, 1985*a*).

Many ultrastructural investigations lead to the conclusion that the Golgi apparatus is involved in the production of the mucilage and its elimination from the protoplast. Numerous dictyosomes are present in the mucilage-secreting cells at the stage of secretion. The presence of polysaccharides in the Golgi vesicles has been proved by histochemical and cytochemical methods (Fig. 8*c*) (Schnepf, 1968; Horner & Lersten, 1968; Rougier, 1972; Trachtenberg & Fahn, 1981; Gedalovitz & Fahn, 1985*a*; Catesson & Moreau, 1985). Many observations lead to the conclusion that Golgi vesicles filled with polysaccharides move towards the cell periphery, where their membranes fuse with the plasmalemma, thus extruding the mucilage to the outside of the protoplast (Trachtenberg & Fahn, 1981; Schnepf, Deichgräber & Barthlott, 1983). The involvement of the ER in polysaccharide mucilage secretion has also been suggested (Horner & Lersten, 1968; Bouchet & Deysson, 1974; Werker & Kislev, 1978; Werker & Fahn, 1981). The mucilage may either accumulate inside the cell wall or in the space between it and the retreating protoplast, as in the mucilage cells of *Opuntia ficus-indica* (Trachtenberg & Fahn, 1981), or be extruded through the cell wall and cuticle to the outside, as in the mucilage-secreting trichomes in *Psychotria* (Horner & Lersten, 1968).

In the secretion of protein–carbohydrate mucilage both the Golgi apparatus and rough ER are involved (Kristen & Lockhausen, 1985). Unzelman & Healey (1974) have observed in the secretory trichome cells of *Pharbitis nil* Benth. ex Miessn., at the stage of secretion, numerous protein–carbohydrate storage vesicles surrounded by a complicated network of RER, and that the two are often in contact with each other. This RER extends to the plasmalemma. These authors suggest that RER and coated Golgi vesicles are active in the export of the mucilage, whereas smooth Golgi vesicles coalesce to form the large storage vesicles. Kristen (1976) suggested that, in the placental papillae of *Aptenia cordifolia*, two types of vacuole enclosed by rough ER play a role in protein–carbohydrate accumulation. One type of vacuole – storage vacuoles – derives from fusion of Golgi vesicles. In the other type, ER cisternae which have lost their membrane-bound ribosomes seem to delimit organelle-free portions of cytoplasm to form pseudovacuoles. Kristen could find no evidence for the export of mucilage via the ER. Joel & Fahn (1980*c*), who studied protein–carbohydrate mucilage secretion in ducts of mango fruits, suggested that areas of cytoplasm rich in ribosomes become delimited by loops of ER to form pseudovacuoles which eventually become bound by a single membrane of ER origin. The protein is probably produced in the pseudovacuoles which become storage bodies. As protein accumulates, carbohydrates are added to these bodies from Golgi vesicles (Fig. 9).

Gum production in ducts of stems of many plant species is usually referred to as *gummosis*. Different views have been expressed regarding the way the gum is produced during gummosis. Some authors attributed gum formation to cell-wall decomposition (Tschirch, 1889; Butler, 1911; Groom, 1926; Vander Mollen, Beckman & Rodehorst, 1977; Stösser, 1979). However, in *Citrus* and some other plants gum production results from the synthetic activity of secretory cells (Catesson *et al.*, 1976; Moreau *et al.*,1978; Catesson & Moreau, 1985; Gedalovich & Fahn, 1985*a*; Morison & Polito, 1985). When gum ducts develop in the cambial region of *Citrus* trees, many active dictysomes containing polysaccharides occur in the epithelial cells. The gum is first secreted into the space between the plasmalemma and the cell wall facing the duct lumen, and then to the outside of the cell wall (Fig. 8*a–c*).

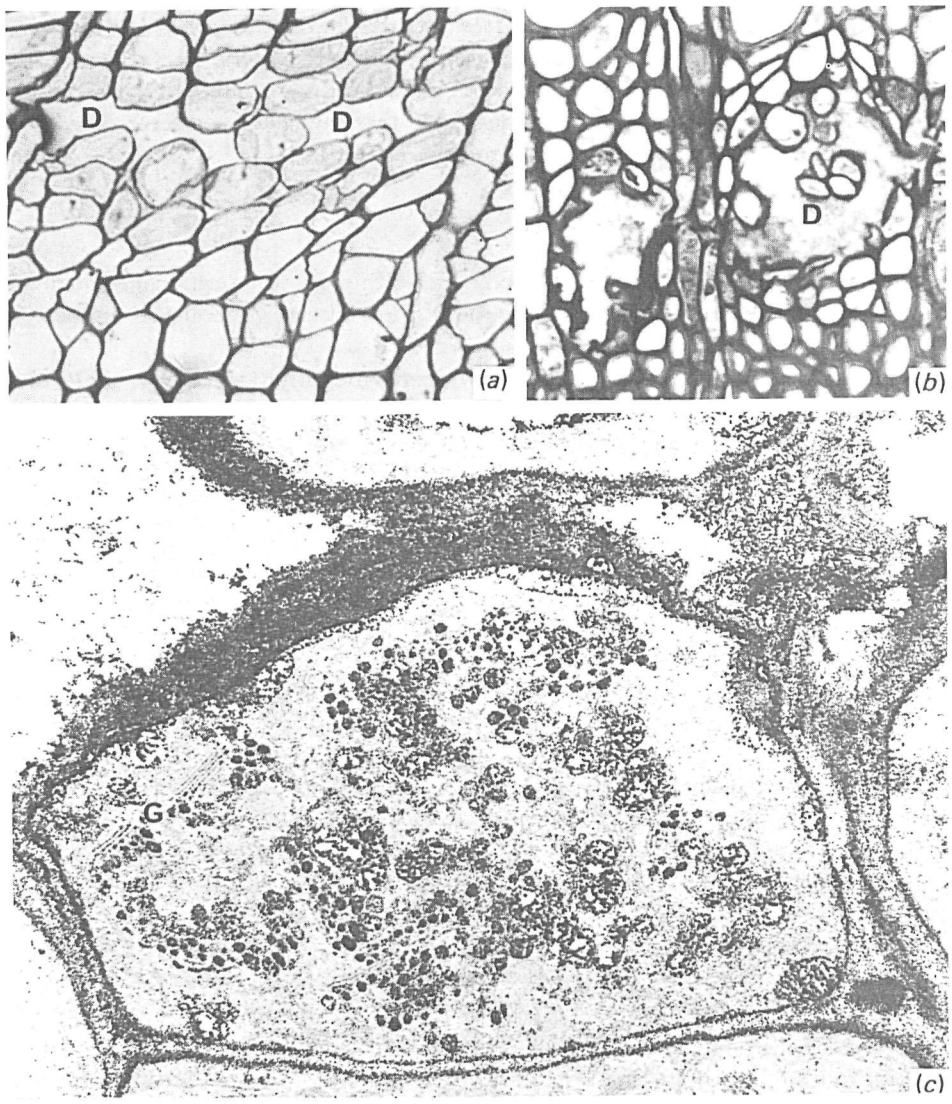

Figure 8. Gum ducts of *Citrus*. (*a*) Young ducts (D) in the cambial region. ×700. (*b*) Ducts embedded in the secondary xylem. ×500. (*c*) Electron micrograph of an epithelial cell stained for polysaccharides; G, Golgi bodies. ×9000. (From Gedalovich & Fahn, 1985*a*.)

V. TISSUES SECRETING LIPOPHILIC MATERIAL

1. *Substances secreted and the cells and tissues involved*

Among the lipophilic materials secreted by plants are terpenes, fats, wax and flavonoid aglycones. Essential oils and resins, which contain a great variety of terpenes (Goodwin & Mercer, 1972), are distinguished only on practical grounds. Essential oils contain volatile low-molecular-weight terpenes, whereas the resins are a mixture of volatile and non-volatile terpenes.

Lipophilic materials are secreted by a variety of anatomical structures; solitary cells – idioblasts (e.g. oil cells of *Laurus*); areas of epidermal cells (e.g. epidermal spots on stipules in buds of *Populus* which secrete flavonoid aglycones mixed with terpenes), trichomes (e.g. glandular trichomes of the Labiatae); cavities (e.g. essential-oil cavities of the Rutaceae); ducts (e.g. resin ducts of *Pinus*). Many tissues secreting lipophilic material may also produce additional substances. The secretory trichomes of *Inula viscosa* Ait., for instance, secrete polysaccharides and protein in addition to lipophilic material.

Fragrance in flowers results from volatile low molecular-weight terpenes, which occur in the form of minute droplets in the cytoplasm of the epidermal and neighbouring mesophyll cells of the sepals (see Kisser, 1958). In some plants e.g. *Ceropegia*, *Aristolochia* and species of the Orchidaceae and Araceae, the fragrance production is restricted to certain areas of the floral parts known as *osmophores* where cells usually differ structurally from their neighbours. In addition to terpenes, osmophores may also secrete amines and ammonia (Vogel, 1962, 1966; Smith & Meeuse, 1966; Pridgeon & Stern, 1983).

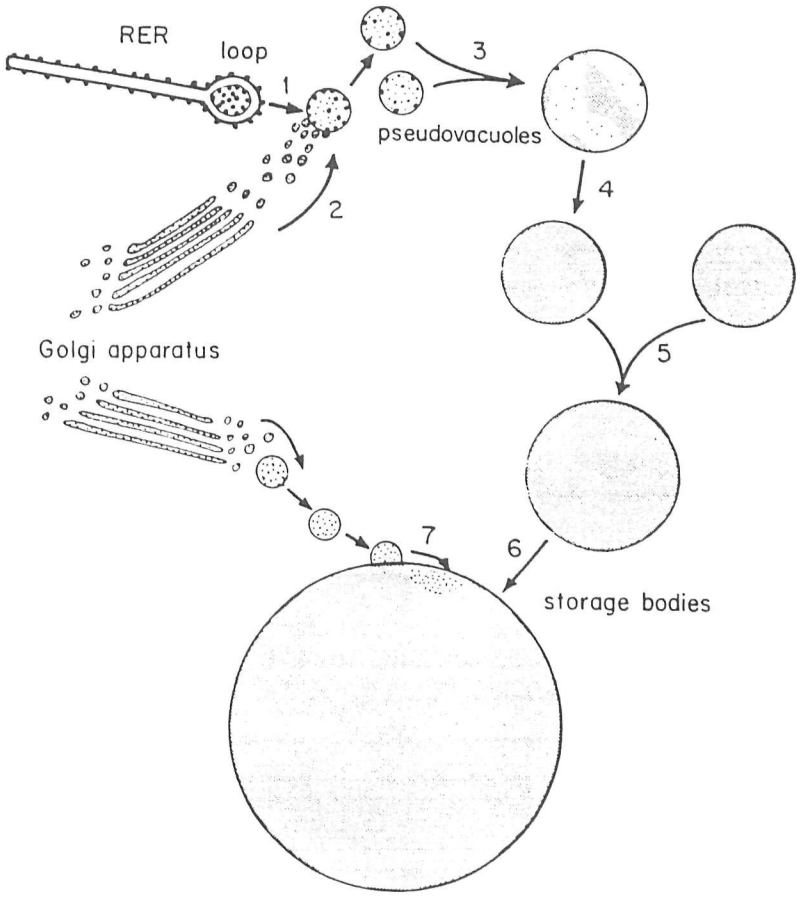

Figure 9. Diagram showing the likely origins of protein–carbohydrate mucilage in mango fruit ducts. (From Joel & Fahn, 1980*c*.)

Oil cells containing oil drops commonly attached to a wall protuberance occur in a number of families, such as Araceae, Aristolochiaceae, Calycanthaceae, Lauraceae, Magnoliaceae, Piperaceae and Saururaceae (Lehmann, 1926; Leemann, 1928; Paech, 1952; Ziegler, 1960; Tucker, 1976; Maron & Fahn, 1979).

Glandular trichomes secreting lipophilic substances occur in many families, e.g. Labiatae Compositae, Geraniaceae, Solanaceae and Cannabinaceae. The trichomes vary in shape and structure. In the Labiatae there are two main types of glandular trichomes, peltate and capitate. Peltate trichomes comprise a basal cell, a short stalk cell and a broad head consisting of many secretory cells arranged in one layer. The capitate trichomes consist of a basal cell, a one- to several-celled stalk and a head of one or two cells (Fig. 10*a b*) (Fahn, 1979*a*; Werker, Ravid & Putievsky, 1985*a*, *b*). The glandular trichomes possess a cuticle proper and a cuticular layer. The side walls of the stalk cells, at least in peltate trichomes, are completely cutinized. With the maturation of the trichomes, the two layers of the cuticle become detached from the pecto-cellulosic wall, and the essential oil accumulates in the subcuticular space. The latter is particularly large in the peltate trichomes. Some of the volatile essential-oil fraction may pass through the cuticle, but most of the secreted material is discharged to the outside only after the rupture of the cuticle (Schnepf, 1969*a*). In some capitate trichomes, pores occur in the cuticle (Amelunxen, 1964). The glandular trichomes of *Cannibus sativa* L. which secretes the narcotic cannabinoids, occur in several forms ranging from few-celled bulbous structures to many-celled capitate glands (Mahlberg *et al.*, 1984).

The secretory trichomes of many compositae are multicellular and biseriate. They may be stalked or sessile. The head consists of one or two pairs of chlorophyll-less summit cells and 2–3 pairs of chlorophyll-containing cells. All head cells secrete other compounds in addition to lipophilic substances. In *Inula viscosa* it has been reported that polysaccharides and proteins occur in addition to lipophilic compounds (Werker & Fahn, 1981). In *Artemisia campestris* L. ssp. *maritima*, fatty acids, terpenes, sterols and flavonol aglycones have been detected (Ascensao & Pais, 1985). The secreted material, as seen in *Inula*, is either exuded through minute pores in the cuticle, or accumulates below the cuticle and is discharged to the outside after the cuticle is ruptured.

For a full account of flavonoid-secreting tissues see Feher (1923), Charrière-Ladreix (1973) and Wollenweber (1984).

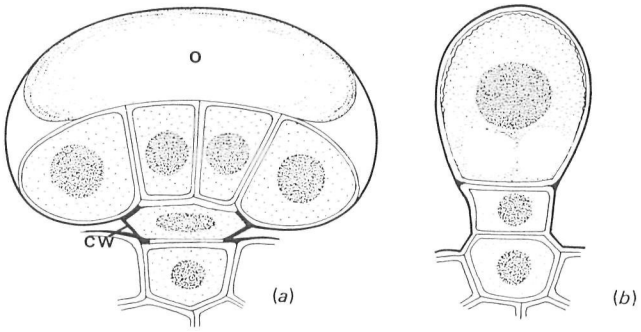

Figure 10. Oil-secreting trichomes of Labiatae. (*a*) A peltate trichome with a secreted oil drop (O) in the subcuticular space; CW, cutinized cell wall. (*b*) capitate trichome.

Secretory cavities occur in many facilities such as Myrtaceae, Rutaceae, Myoporaceae, Hypericaceae and in some species of the Leguminosae (Metcalfe & Chalk, 1983). *Secretory ducts (or canals)* are known to occur in the Pinaceae, Anacardiaceae, Compositae, Hypericaceae, Leguminosae and Umbelliferae (Metcalfe & Chalk, 1983).

Several cell layers usually line the lumen of ducts and cavities. The innermost layer is most active in the process of secretion and is called the epithelium. During the expansion of the cavity, cells of the outer layers may become incorporated into the epithelium (Werker & Fahn, 1969; Fahn & Evert, 1974; Joel & Fahn, 1980*a*; Bosabalidis & Tsekos, 1982*a*; Pereira da Costa, 1985). The outermost cell layers of the secretory complex may be thick-walled and form a protective sheath, as for instance in *Citrus* (Bosabalidis & Tsekos, 1982*a*). In the resin ducts of *Pinus* the epithelial cells are thin-walled, but outside them is a sheath of one or more layers of cells with relatively thick walls. Within the sheath are dead cells which may form a cylinder around the epithelial cells. The inner lamellae of the wall of these dead cells contain suberin (Werker & Fahn 1969).

The epithelial cells of the secretory cavities (Fig. 11*a*, *b*) and ducts discharge the secreted materials into the lumina of these structures. The manner in which these lumina develop in the various organs of different plant species has been widely discussed. Views as to whether the lumen of a certain cavity or duct develops lysigenously or schizogenously, or by a schizo-lysigenous process, have often been contradictory (Carr & Carr, 1970; Fahn & Joel, 1977; Joel & Fahn, 1980*a*; Bosabalidis & Tsekos, 1982*a*). The cells of the cavities and ducts which are about to disintegrate usually have a highly osmiophilic cytoplasm, and often the dictyosomes and/or the ER become dilated (Amelunxen & Arbeiter, 1967; Fahn & Benouaiche, 1979; Joel & Fahn, 1980*a*; Bosabalidis & Tsekos, 1982*a*).

2. *Cell compartments involved in the process of secretion*

The most common ultrastructural feature of the cells secreting a lipophilic substance is the occurrence of osmiophilic material in plastids. In most cases these plastids are partly or completely surrounded by endoplasmic reticulum (Fig. 11*c*) (periplastidal ER) (Schnepf, 1969*b*; Fahn & Evert, 1974; Fahn & Benayoun, 1976; Joel & Fahn, 1980*b*; Bosabalidis & Tsekos 1982*a*; Heinrich & Schultze; 1985). In some plants the plastids contain a peripheral reticulum which may function in the transport of lipophilic material to the envelope (Vermeer & Peterson, 1979; Werker & Fahn, 1981; Ascensao & Pais, 1985). Plastids with a peripheral reticulum occur also in floral chromoplasts of some plants (Whatley & Whatley, 1987). The membranes of the ER in contact with osmiophilic droplets are usually smooth. Smooth tubular ER often occurs in the cytoplasm (Amelunxen & Arbeiter, 1967; Schenpf, 1960*b*, 1972; Joel & Fahn, 1980*b*; Danilova & Kashina, 1987). In addition to the plastids and the ER, osmiophilic material has also been observed in mitochondria, dictyosomes and the nuclear envelope (Vassilyev, 1970; Fahn & Evert, 1974; Fahn & Benayoun, 1976; Joel & Fahn, 1980*b*). Production of lipophilic material in the ground cytoplasm has been suggested in the calyx glands of *Plumbago capensis* Thunb. (Rachmilevitz & Joel, 1976) and in oil glands of *Origanum dictamnus* L. (Bosabalidis & Tsekos, 1982*b*).

The occurrence of osmiophilic material in several different cell compartments in tissues which secrete essential oils or resins raises several questions regarding the possible site(s) of synthesis of these materials. Three possible interpretations can be suggested. (1) Each organelle in which osmiophilic droplets occur is capable of synthesizing all the oil or resin components independently. (2) There are several steps in essential-oil or resin synthesis, each taking place in a particular organelle. (3) Different components are synthesized by different organelles. On the basis of the fact that, in the resin ducts of *Mangifera indica* L., the lipophilic droplets associated with the dictyosomes appeared less osmiophilic than those in the plastids and the ER,

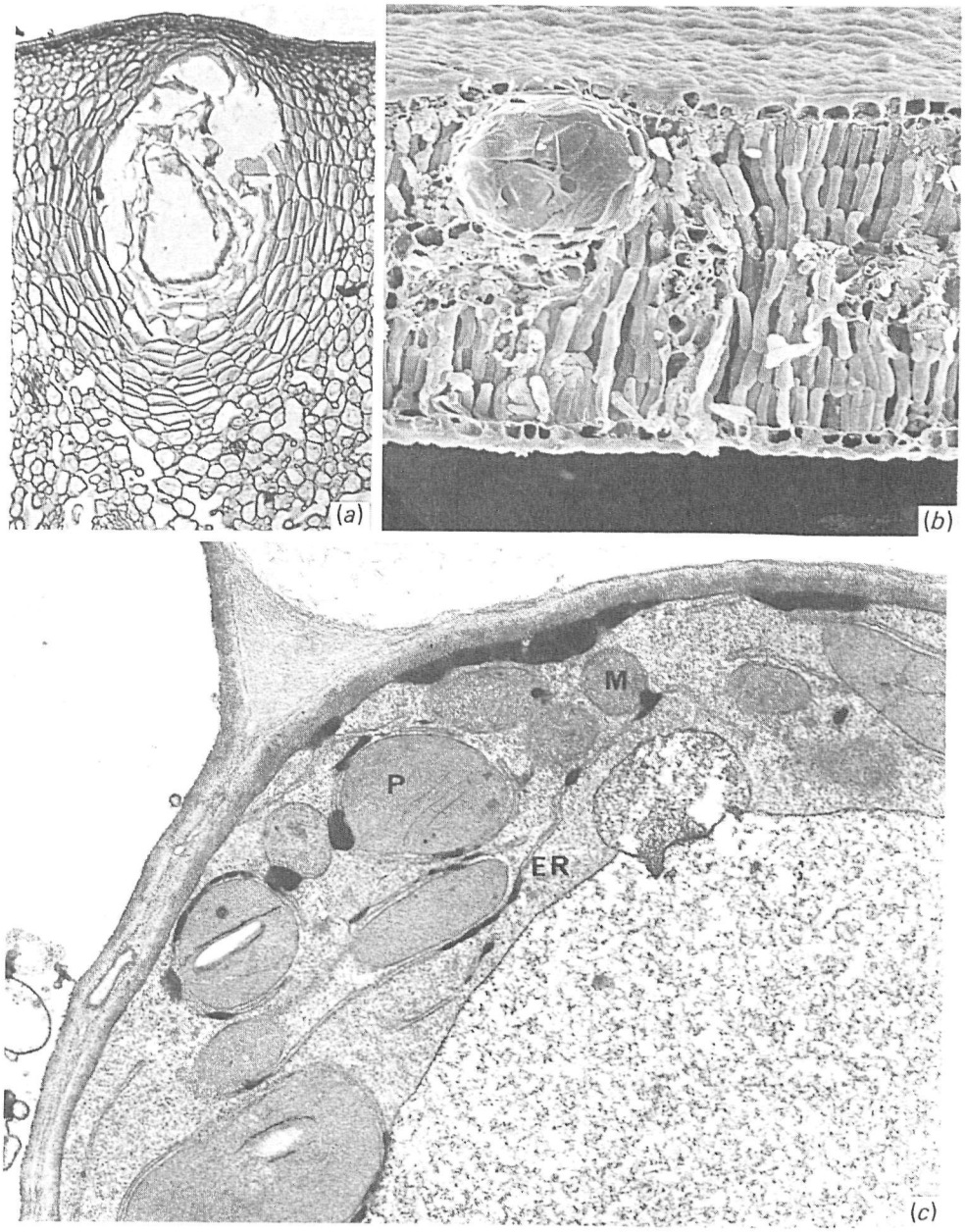

Figure 11. (*a*, *b*) Oil cavities. (*a*) An oil gland in a *Citrus* pericarp. × 50. (*b*) An oil gland in a *Eucalyptus* leaf (scanning electron micrograph). × 150. (*c*) Electron micrograph of an epithelial cell of a primary resin duct of *Pinus halepensis* Mill.; M, mitochondrion; P, plastid. × 28000. (*a* and *b* from Fahn, 1982; (*c*) from Benayoun & Fahn, 1979.)

and that both kinds of droplets were also found outside the plasmalemma, Joel & Fahn (1980*b*) suggested that the third interpretation was the most likely in this case. This view is strengthened by the results of a histochemical study which revealed droplets of different kinds in the shoot apical region of *Pinus halepensis* (Werker & Fahn, 1968).

Cheniclet & Carde (1985) suggested that there is a relationship between the structure of the plastids and their involvement in monoterpenes synthesis. When the essential oil contains significant amounts of monoterpenes, the secretory cells contain typical leucoplasts devoid of ribosomes and thylakoids. In contrast, when the volatile extract contains no monoterpene, or only a small amount, the plastids display various structural characteristics such as thylakoids, ribosomes and tubular networks.

The ER in addition to taking part in the synthesis of lipophilic substances, may also take part in intracellular transport of this material (Figs. 11*c* & 12) (Benayoun & Fahn, 1979; Bosabalidis & Tsekos, 1982*a*). Benayoun & Fahn (1979) and Mikulska & Zolnierowicz (1976) observed connections between membranes of the plastidal envelope and the periplastidal ER. Benayoun & Fahn (1979) suggested that, in the epithelial cells of the resin ducts of *Pinus halepensis*, the ER is transporting the resin components from

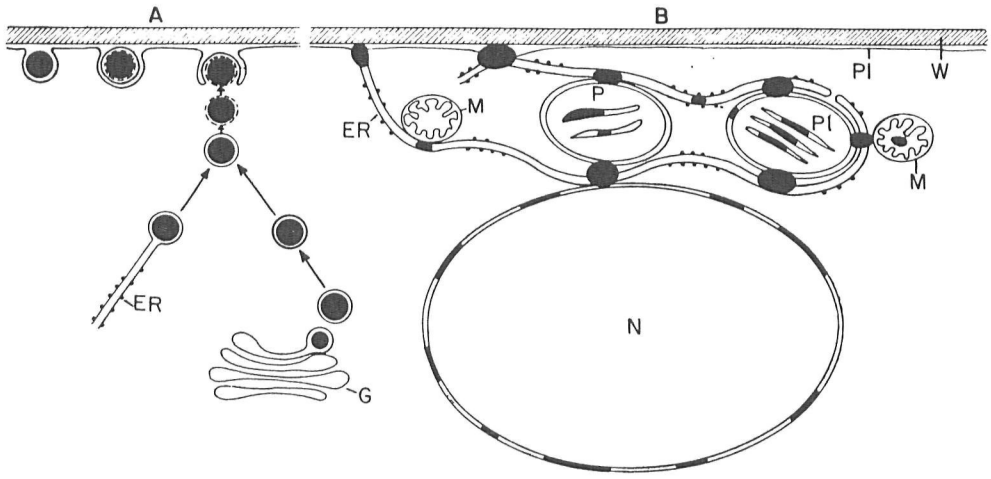

Figure 12. Diagram showing the possible mode of intracellular transport of resin and its elimination from the protoplasts of epithelial duct cells; ER, endoplasmic reticulum; G, Golgi body; M, mitochondrion; P, plastid; Pl, plasmalemma; W, cell wall; solid black indicates resin droplets.

the plastids, mitochondria and nuclear envelope to the plasmalemma. By fusing with the plasmalemma the ER releases the resin to the outside of the protoplast. The resin produced in the cytoplasm and by the Golgi apparatus may be eliminated by plasmalemma invaginations, which surround the resin droplets and detach them from the protoplast (Fig. 12). Fusion of membranes of the ER, which carries oil droplets, with the plasmalemma has also been suggested by Bosabalidis & Tsekos (1982*a*) for the secretory cells of the essential-oil cavities of *Citrus deliciosa* Tenore. Transport of fatty oils through the plasmalemma via granulocrine elimination has also been postulated in the osmophores of the orchid *Restrepia* (Pridgeon & Stern, 1983).

VI. FACTORS INFLUENCING THE DEVELOPMENT OF CERTAIN SECRETORY TISSUES

1. *General background*

Glandular trichomes are constant features of many plant species and develop without external stimuli. The question as to whether external factors influence their density on the plant surface has not yet been studied.

The inner secretory tissues, such as ducts and cavities, are also characteristic of certain plants but their development may or may not depend on external factors, such as injuries, pathogens or physiological stresses (Fahn, 1987*b*).

2. *Resin ducts*

In the Pinaceae, resin ducts are regarded as a normal feature in the genera *Pinus*, *Picea*, *Larix* and *Pseudotsuga*, whereas in *Abies*, *Cedrus*, *Tsuga* and *Pseudolarix* they were reported to develop only as a result of injury (Fig. 13*a*, *b*).

An investigation carried out on *Cedrus libani* (Fahn, Werker & Ben-Zur, 1979) revealed that not only wounds, but also exogenous auxin induce the formation of resin ducts in the secondary xylem of this plant. Ducts were formed if the cambium was active within the period between auxin application and branch removal. Ducts were also formed when cambial activity commenced during the period of the experiment, even after a period of 3–4 months.

In *Pinus*, where duct formation occurs normally in the secondary body, wounding, pressure, exposure to wind or the application of auxin causes an increase in the number of secondary resin ducts (Fahn & Zamski, 1970). It seems possible that the so-called normally occurring ducts in the secondary body of *Pinus* also develop as a result of external stimuli, but their sensitivity threshold is much lower than that of *Cedrus*.

3. *Gum ducts*

Gum-duct formation is known to occur in many plants, e.g. in the Prunoideae, *Brachychiton*, *Citrus*, *Acacia* species and many others. Different views have been expressed regarding the development of these ducts. Gummosis in the Prunoideae, for instance, was considered by some authors to be primarily a response to

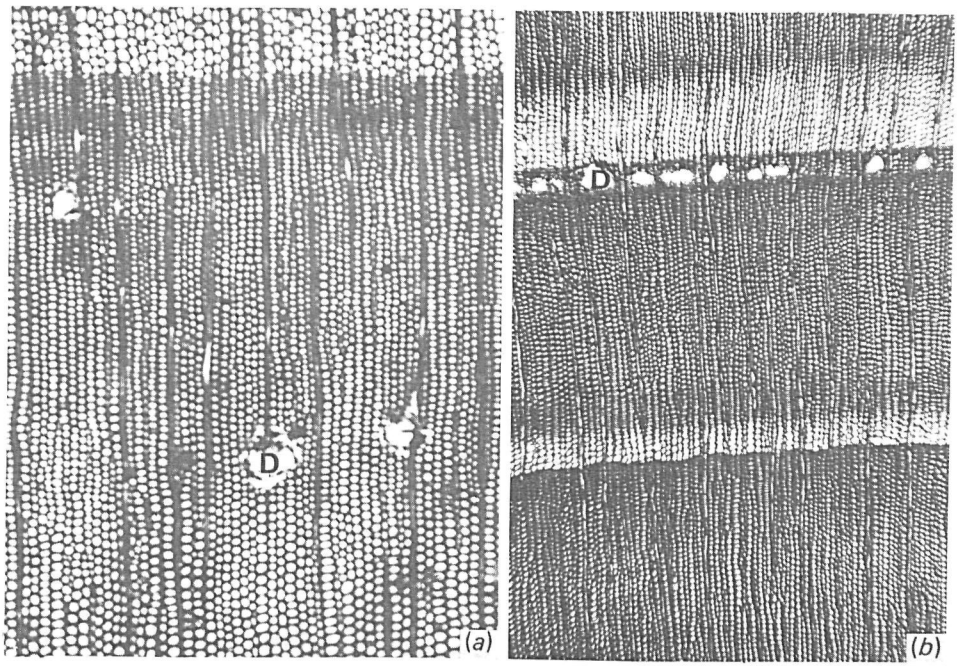

Figure 13. Transverse sections of conifer secondary xylem; (*a*) *Pinus halepensis*. ×40. (*b*) *Cedrus libani*. L. Barrel. D, resin duct. ×35.

injury or to pathogen attack (Ceruti & Scurti 1954*a*, *b*), while others suggested that it is a natural phenomenon which is intensified by injury or pathogen infection (Grosclaude 1966; Morrison & Polito, 1985).

Gum ducts in *Citrus* trees develop in response to fungal and viral diseases. The well-known 'brown rot' gumosis of *Citrus* trees is caused by the fungus *Phytophthora citrophthora* (Sm. & Sm) Leon. When *Citrus* trees were artificially infected with this fungus, gum ducts began to develop schizogenously in the cambium (Fig. 8*a*). With the continuing activity of the cambium and differentiation of xylem, the gum ducts became embedded in the latter (Fig. 8*b*) and the activity of the epithelial cells ceased. The cell wall of many epithelial cells broke and the gum still present in the cells was released (Gedalovich & Fahn, 1985*a*).

Another type of gummosis is the occlusion of vessels with gum-like material. This may occur in response to physiological stresses arising from wounding or infection. The vascular occlusions in the roots of cassava (*Manihot esculenta* Crantz) may develop in response to wounding, and appear to be intensified when roots are stored at low humidity (Rickard & Gahan, 1983). In a number of plants, e.g. *Dianthus caryophyllus* L., *Ulmus campestris* L. and *Ailanthus excelsa* Roxb., it has been reported that the vascular occlusions develop in response to infection by fungi (Catesson & Moreau, 1985; Shah & Babu, 1986).

In *Dianthus* it has been shown that as a result of infection, living cells in contact with vessels acquire secretory functions. They secrete carbohydrates, glycoproteins and polyphenols into the damaged vessels and occlude them. It has been suggested that the polysaccharides and the glycoproteins are secreted through the Golgi apparatus and that the polyphenols are synthesized by the ER (Catesson *et al.*, 1976; Catesson & Moreau, 1985).

In *Ailanthus excelsa*, according to Shah & Babu (1986), the vascular occlusions contain polysaccharides, lipids, protein, phenolics, lignin and probably also pectins. All the inclusion components except lignin and pectin were postulated, by these authors, to be produced by the cells in contact with vessels.

4. *The effects of ethylene on duct formation*

Experiments involving application of ethrel, 1-amino-cyclopropan-1-carboxylic acid (ACC) and auxins to branches of *Citrus* trees showed that these substances cause the formation of gum ducts in a manner similar to that caused by the fungus *Phytophthora citrophthora* (Gedalovich & Fahn, 1985*b*). Ethrel was found to be the most effective substance. Ethrel (0·05 %) in water induced the formation of gum ducts of the same length as those formed after infection with the fungus, that is 3–5 cm above and below the infected or treated wound. When higher concentrations of ethrel were used, much longer gum ducts were formed (up to 15 cm). The rate of cambial activity at the time of application affected the response of the branches to ethrel and to a greater extent the response to auxin.

Stem segments artificially infected with the fungus were found to release ethylene. As gum ducts were also formed in response to ACC, which is a precursor of ethylene in higher plants and not in fungi, it appears that the production of ethylene by the infected stem tissue is a factor which directly influences gum-duct production in the *Citrus* trees.

Recently Yamamoto, Kozlowski & Wolter (1987) found that the flooding of *Pinus halepensis* seedlings caused an increase in the formation of the longitudinal resin ducts in the secondary xylem, and that the flooding also stimulated ethylene production by the immersed stems. Yamamoto & Kozlowski (1987*a*) reported that 1% ethrel also stimulated an increase in the number of resin ducts in the xylem of seedlings of this species. In seedlings of *Pinus densiflora* Sieb. & Zucc., flooding did not induce the formation of resin ducts, but ethrel did (Yamamoto & Kozlowski, 1987*b*).

It should be mentioned that many effects previously considered to be induced directly by auxin are now known to be a result of auxin-induced ethylene formation (Abeles, 1973; Jones & Kende, 1979; Yang *et al.*, 1980; Imaseki, Yoshii & Todaka, 1982). The effect of auxin on the formation of resin ducts in *Pinus halepensis* observed by Fahn & Zamski (1970) and in *Citrus* by Gedalovich & Fahn (1985*b*) may thus be a result of auxin-induced ethylene formation.

VII. EVOLUTIONARY CONSIDERATIONS

Secretory structures have often been taken into consideration in taxonomic studies, relatively little attention has been paid to the evolutionary aspects of these structures, though phylogenetic trends in the localization of nectaries have been suggested by some authors.

1. *Nectaries*

The localization of nectaries in plants is of phylogenetic interest. Extrafloral nectaries occur not only in the angiosperms but also in several genera of ferns e.g. *Angiopteris*, *Cyathea*, *Hemitelia*, *Platycerium* and *Pteridium* (Bonnier, 1879; Darwin, 1877; Figdor, 1891; Dümmer, 1911). Frey-Wyssling (1933) expressed the view that, in the course of evolution, the extrafloral nectaries preceded the floral nectaries. It has been suggested that the sugar-containing droplets, exuded by the micropyle of flowers of the Gnetophyta, play a role in pollination (Meeuse, 1978).

Floral nectaries in the angiosperms are found on a variety of the flower parts (Fahn, 1953, 1979*a*) ranging from the sepals to petals, stamens, the receptacle, ovary and style. On these organs they may be situated in different places. Ovarial nectaries occur in some plants on the surface of the ovary (e.g. in *Limnocharis*) whereas in others they are deeply sunk in the ovary (e.g. septal nectaries in many monocotyledons). Stylar nectaries may occur at the base of the style (e.g. in species of Umbelliferae and Compositae), or on the stigma (e.g. in *Arum* and *Asclepias*). Staminal nectaries may be present on the filaments (e.g. in *Colchicum*, *Laurus* and *Dianthus*), or as appendages on connectives (e.g. in *Viola*).

Examination of the position of the nectaries in the flowers of the various families suggests the existence of a phylogenetic trend whereby the nectary is shifted in a centri-acropetal direction, i.e. from the outer towards the inner floral parts, and towards the upper regions of the gynoecium (Brown, 1938; Fahn, 1953; Daumann, 1930, 1970; Kartashova, 1965; Smets, 1986). Recently, Magin (1983) suggested that in the Umbelliferae there exist two main phylogenetic trends of nectary movement, as follows. (1) Centrifugal shift to the axial part of the peripheral phyllomes and/or to the axial parts of the gamophyllous pedestal. (2) An acrocentric shift to the upper dorsal parts of the style. The trichomatous nectaries, generally occurring outside the androecium of some Cucurbitaceae species, were suggested by Vogel (1981) to have evolved as a result of the contraction of the central part of the flower.

2. *Resin ducts in the secondary xylem*

In all conifers resin ducts are present in the primary tissues. However, in the Pinaceae they are also present in the secondary tissues. In this family, as noted previously, plants of some genera produce resin ducts in the secondary tissues without external stimuli, while in other genera the resin ducts are formed only in response to external factors.

Penhallow (1907) considered the development of resin ducts in the secondary xylem of the Pinaceae as specialization. He suggested that in the primitive condition parenchyma cells were scattered throughout the secondary xylem. These cells then became aggregated, and resin cysts, such as those found in *Abies* and *Tsuga*, were formed (see Fig. 13*b*). From cysts, resin ducts such as those occurring in *Pinus* were derived (Fig. 13*a*).

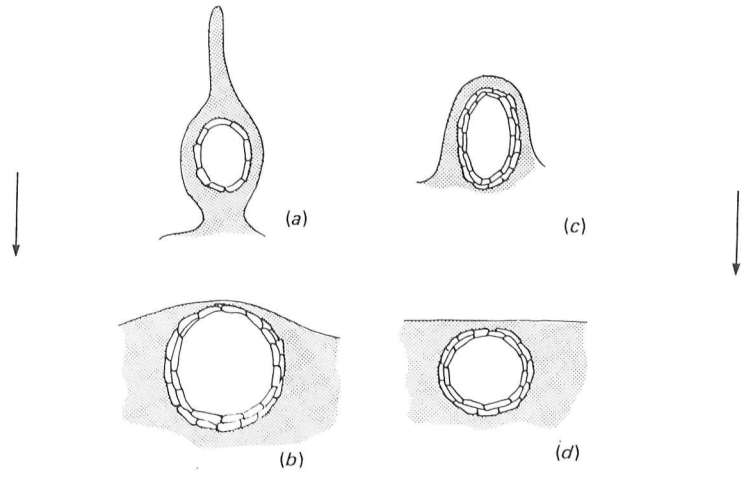

Figure 14. Diagram showing a possible evolutionary trend in the development of glandular trichomes containing oil cavities in *Dictamnus albus* L. (*a*, *b*) and *Eucalyptus citriodora* (c, d).

Jain (1976) supported Penhallow's view on the basis of a study of eastern Himalayan Pinaceae and from data of other authors on fossil gymnosperm wood. According to these data no ducts were found in woods from Carboniferous, Permian or Triassic strata. The first vertical resin ducts were seen in coniferous woods from the Mid Jurassic. In these fossil woods only a few resin ducts were observed in tangential series. In a number of *Protopiceoxylon* forms of somewhat later age (Upper Jurassic and Lower Cretaceous) scattered resin ducts were found in addition to those occurring in tangential series. Jain further stated that with the exception of 'the doubtful *Pityoxylon eiggense*', pine-like woods have not been recognized in strata below the lower Cretaceous. In *Pityoxylon*, too, the resin ducts are in tangential series, indicating therefore a possible relation to *Larix*, *Pseudotsuga* and *Picea*. The fossil data thus indicate that the localization and restricted distribution of resin ducts preceded the scattered and widely dispersed type, such as found in *Pinus* (Fig. 13*a*). The vertical resin ducts of *Cedrus*, *Abies*, *Tsuga* and *Pseudolarix*, which develop in response to outer stimuli, occur in tangential rows (Fig. 13*b*).

3. *Secretory trichomes*

Denissova (1975) suggested a classification of terpenoid-secreting tissues according to their progressive evolution. She distinguished four types of terpens-secreting tissue and deduced that they originally evolved from unspecialized parenchyma cells. These types are: (1) endogenous secretory tissues with intracellular accumulation of secreted material; (2) schizogenous endogenous secretory tissues with extracellular accumulation of secreted material; (3) secretory tissues with a schizo-lysigenous lumen; (4) exogenous glandular structures (glandular trichomes). The latter type was regarded as the most recently evolved.

In the various organs of many pteridophytes are secretory ducts, which usually secrete mucilage or gums. In some pteridophytes the terminal cells of hairs may become glandular (Ogura, 1972). In the rhizome and leaf bases of *Dryopteris* species, glandular hairs occur in intercellular spaces. These hairs secrete phloroglucinol derivatives (Huurre, Huhtikagas & Widen, 1979). Similar hairs occur also on the epidermis of the rhizome. It is of interest to mention that in *Dryopteris fragrans* (*L.*) Schott, the inner glandular hairs are sparse but the rhizome epidermis is densely covered by a glandular tomentum (Widen & Britton, 1969).

In contrast to resin ducts, glandular hairs are rare in conifers and have been reported only on juvenile leaves of *Pinus cembra* L. and *P. lambertiana* Dougl. (Napp-Zinn, 1966).

In the dicotyledons all types of secretory tissues are very common, including glandular trichomes. However, the latter do not occur in most of the woody Ranales.

In some dicotyledonous families, e.g. in the Myrtaceae and Rutaceae, oil cavities occur in the cortex of the stems and in the leaves. In *Eucalyptus citriodora* Hook and *E. torellina* F.v.M. (Farooqui, 1979–80) and *Dictamnus albus* L., trichomes that include oil cavities are present. Brocheriou (1976) suggested that the oil-cavity-bearing emergences on young leaves of *Eucalyptus citriodora* preceded, in evolution, the oil cavities occurring within the leaves. Denissova (1976) expressed an opposing view regarding the evolution of the oil-cavity-bearing trichomes. She suggested that the *Dictamnus* glands developed from oil cavities within the organs of the Rutaceae. I am inclined to accept Denissova's view in relation to the emergences in *Eucalyptus citriodora* (Fig. 14).

Trichome nectaries also appear to be more advanced structures than those in which the bulk of the

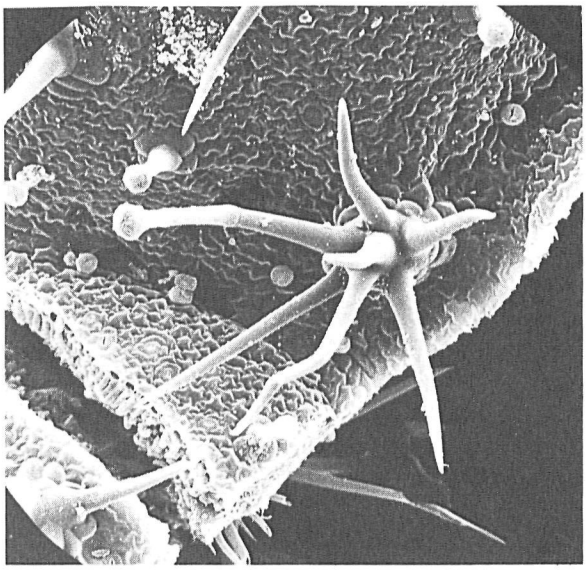

Figure 15. Scanning electron micrograph of a branched trichome on a leaf of *Phlomis viscossa* Poir. At the end of one of its branches there is a glandular head. ×110.

secretory cells occur below the epidermis, and where the nectar is secreted through stomata or lysogenous cavities.

It has been suggested that the glandular trichomes of a number of plant species developed phylogenetically from non-glandular trichomes Fedorowicz, in Uphof, 1962; Fahn & Shimony, 1977; Fahn, 1979*a*). In *Avicennia marina* (Forskål) Vierh., glandular and non-glandular trichomes are present. Both types of trichome are initiated and develop similarly up to the stage of a three-celled primordium. From this stage, differences between the two types begin to appear (Fahn & Shimony, 1977). The non-glandular trichomes of *Avicennia* species vary in the number of cells, from 3 to 5; in the glandular trichomes of *A. marina* there are 11–17. It has therefore been suggested that the phylogenetic sequence was from very few-celled to several-celled non-glandular trichomes and then to glandular trichomes.

In some species of the Labiatae (e.g. *Phlomis* spp. and *Rosmarinus officinalis* L.) there occur both branched non-glandular trichomes and similar trichomes in which one of the branches carries a glandular head (Fig. 15) (Azizia & Cutler, 1982; Werker, Ravid & Putiersky, 1985*a*).

In summary, the following trends in the evolution of the secretory tissues are suggested: (1) During the course of evolution secretory tissues first developed inside plant organs. (2) In the primitive conditions only secretory idioblasts or groups of such cells were scattered among the cells of the ordinary tissues. (3) Later, secretory ducts and cavities developed. (4) The glandular trichomes are the most recently evolved secretory structures.

REFERENCES

Abeles, F. B. (1973). *Ethylene in Plant Biology*. Academic Press, New York.

Amelunxen, F. (1964). Elektronen mikroskopische Untersuchungen an den Drüsenhaaren von *Mentha piperita*. *Planta Medica* **12**, 121–139.

Amelunxen, F. (1967). Einige Beobachtungen in den Blattzellen von *Mentha piperita* L. *Planta Medica* **15**, 32–34.

Amelunxen, F. & Arbeiter, H. (1967). Untersuchungen an den Spritzdrüsen von *Dictamnus albus* L. *Zeitschrift für Pflanzenphysiologie* **60**, 156–168.

Ascensao, L. & Pais, M. S. S. (1985). Différenciation et processus sécréteur des trichomes d'*A. campestris* ssp. *maritima* (Compositae). *Annales des Sciences Naturelles, Botanique*, 13e série **7**, 149–171.

Azizia, D. & Cutler, D. F. (1982). Anatomical, cytological and phytochemical studies on *Phlomis* L. and *Eremostachys* Bunge (Labiatae). *Botanical Journal of the Linnean Society* **85**, 249–281.

Baas, P. & Gregory, M. (1985). A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurrence with mucilage cells. *Israel Journal of Botany* **34**, 167–186.

Bahadur, B., Chaturvedi, A. & Swamy, N. R. (1986). Nectar types in Indian plants. *Proceedings of the Indian Academy of Science (Plant Science)* **96**, 41–48.

Baker, H. G., Baker, I. (1973*a*). Amino-acids in nectar and their evolutionary significance. *Nature* **241**, 543–545.

BAKER, H. G. & BAKER, I. (1973*b*). Some autecological aspects of the evolution of nectar-producing flowers, particularly amino acid production in nectar. *In*: *Taxonomy and Ecology* (Ed. by V. H. Heywood), pp. 243–264. Academic Press, London.

BAKER, H. G. & BAKER, I. (1975). Studies of nectar-constitution and pollinator–plant coevolution. In: *Coevolution of Animals and Plants* (Ed. by L. E. Gilbert & P. H. Raven), pp. 100–140. University of Texas Press, Austin.

BAKER, H. G. & BAKER, I. (1983*a*). A brief historical review of the chemistry of floral nectar. In: *Biology of Nectaries* (Ed. by B. Bentley & T. Elias), pp. 126–152. Columbia University Press, New York.

BAKER, H. G. & BAKER, I. (1983*b*). Floral nectar sugar constituents in relation to pollinator type. In: *Handbook of Experimental Pollination Biology* (Ed. by C. E. Jones & R. J. Little), pp. 117–141. Scientific and Academic Edition, Van Nostrand Reinhold, New York.

BAKER, D. A., HALL, J. L. & THROP, J. R. (1978). A study of the extrafloral nectaries of *Ricinus communis*. *New Phytologist* **81**, 129–137.

BEHRENS, W. J. (1879). Die Nectarien der Blüten. *Flora* **62**, 2–11, 17–27, 49–54, 113–123, 145–153, 233–240, 241–247, 305–314, 369–375, 433–457.

BELIN-DEPOUX, M. & CLAIR-MACZULAJTYS, D. (1975). Introduction à l'étude des glandes foliaires de l'*Aleurites moluccana* Willd. II. Aspects histologiques de la glande pétiolaire fonctionnelle. *Revue générale de Botanique* **82**, 119–155.

BENAYOUN, J. & FAHN, A. (1979). Intracellular transport and elimination of resin from epithelial duct-cells of *Pinus halepensis*. *Annals of Botany* **43**, 179–181.

BENNER, U. & SCHNEPF, E. (1975). Die Morphologie der Nectarausscheidung bei Bromeliaceen, Beteiligung des Golgi Apparates. *Protoplasma* **85**, 337–349.

BENTLEY, B. L. (1976). Plants bearing extrafloral nectaries and the associated ant community, interhabitat differences in the reduction of herbivore damage. *Ecology* **57**, 815–820.

BENTLEY, B. L. (1977). Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* **8**, 407–427.

BIELESKI, R. L. & REDGWELL, R. J. (1980). Sorbitol metabolism in nectaries from flowers of Rosaceae. *Australian Journal of Plant Physiology* **7**, 15–25.

BLACK, R. F. (1954). The leaf anatomy of Australian members of the genus *Atriplex*. *Australian Journal of Botany* **2**, 269–286.

BONNIER, G. (1879). *Les nectaires*. Thèse, Faculty of Science, Paris.

BOSABALIDIS, A. M. & THOMSON, W. W. (1984). Ultrastructural differentiation of an unusual structure lining the anticlinal walls of the inner secretory cells in *Tamarix* salt glands. *Botanical Gazette* **145**, 427–435.

BOSABALIDIS, A. & TSEKOS, I. (1982*a*). Ultrastructural studies on the secretory cavities of *Citrus deliciosa* Ten. II. Development of the oil-accumulating central space of the gland and process of active secretion. *Protoplasma* **112**, 63–70.

BOSABALIDIS, A. & TSEKOS, I. (1982*b*). Glandular scale development and essential oil secretion in *Origanum dictamnus* L. *Planta* **156**, 496–504.

BOUCHET, P. & DEYSSON, G. (1974). Les canaux à mucilage des Angiospermes. Etude morphologique et ultrastructurale des cellules constituant les canaux à mucilage du *Sterculia bidwilli* Hook. *Revue générale de Botanique* **81**, 369–402.

BROCHERIOU, J. (1976). Contribution à l'étude ontogénique des émergences chez l'*Eucalyptus citriodora* Hook. (Myrtaceae). *Revue générale de Botanique* **83**, 313–329.

BROWN, W. H. (1938). The bearing of nectaries on the phylogeny of flowering plants. *Proceedings of the American Philosophical Society* **79**, 549–595.

BUTLER, O. (1911). A study of gummosis of *Prunus* and *Citrus*, with observations on squamosis and exanthema of *Citrus*. *Annals of Botany* **25**, 107–153.

CAMPBELL, N. & THOMSON, W. W. (1976*a*). The ultrastructure of *Frankenia* salt glands. *Annals of Botany* **40**, 681–686.

CAMPBELL, N. & THOMSON, W. W. (1976*b*). The ultrastructural basis of chloride tolerance in the leaf of *Frankenia*. *Annals of Botany* **40**, 687–693.

CARR, D. J. & CARR, S. G. M. (1970). Oil glands and ducts in *Eucalyptus* L'Hérit. II. Development and structure of glands in the embryo. *Australian Journal of Botany* **18**, 191–212.

CASPARY, R. DE (1848). *De Nectariis*. Elberfeld.

CATESSON, A., CZANINSKI, Y., PERESSE, M. & MOREAU, M. (1976). Sécrétions intravasculaires de substances 'gommeuses' par les cellules associées aux vaisseaux en réaction à une attaque parasitaire. *Bulletin de la Société Botanique de France* **123**, 93–107.

CATESSON, A. M. & MOREAU, M. (1985). Secretory activity in vessel contact cells. *Israel Journal of Botany* **34**, 157–165.

CECCHI FIORDI, A. & PALANDRI, M. R. (1982). Anatomic and ultrastructural study of the septal nectary in some *Tillandsia* (Bromeliaceae) species. *Caryologia* **35**, 477–489.

CERUTI, A. & SCURTI, J. (1954*a*). Sulla formazione delle gomme nel ciliegio (*Prunus avium* L.). I. Morfologia. *Annali della Sperimentazione Agraria* **8**, 489–499.

CERUTI, A. & SCURTI, J. (1954*b*). Sulla formazione delle gomme nel ciliegio (*Prunus avium* L.). II. Istochimica. *Annali della Spermentazione Agraria* **8**, 501–518.

CHAPMAN, V. J. (1944). The morphology of *Avicennia nitida*. *Botanical Journal of the Linnean Society* **52**, 487–533.

CHARRIÈRE-LADREIX, Y. (1973). Etude de la sécrétion flavonoidique des bourgeons de *Populus nigra* L., modifications ultrastructurales des trichomes au cours du processus glandulaire. *Journal de Microscopie et de Biologie Cellulaire* **24**, 75–90.

CHENICLET, C. & CARDE, J. P. (1985). Presence of leucoplasts in secretory cells and of monoterpenes in the essential oil: a correlative study. *Israel Journal of Botany* **34**, 219–238.

CHRIST, P. & SCHNEPF, E. (1985). The nectaries of *Cynanchum vincetoxicum* (Asclepiadaceae). *Israel Journal of Botany* **34**, 79–90.

CRUDEN, R. W., HERMANN, S. M. & PETERSON, S. (1983). Patterns of nectar production and plant–pollinator coevolution. In: *Biology of Nectaries* (Ed. by B. Bentley & T. Elias), pp. 80–125. Columbia University Press, New York.

DANILOVA, M. F. & KASHINA, T. K. (1987). Ultrastructure of glandular scales in *Perilla ocymoides* (Lamiaceae) in connection with their possible involvement in the synthesis of steroid hormones and gibberellins. *Botanicheskii Zhurnal SSSR* **72**, 427–435. (In Russian)

DARWIN, C. (1876). *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*. John Murray, London.

DARWIN, F. (1877). On the nectar glands of the common brakefern. *Botanical Journal of the Linnean Society* **15**, 407–409.

DAUMANN, E. (1930). Das Blütennektarium von *Magnolia* und Futterkörper in der Blüte von *Calycanthus*. *Planta* **11**, 108–116.

DAUMANN, E. (1970). Das Blütennektarium der Monocotyledonen unter besonderer Berücksichtigung seiner systematischen und phylogenetischen Bedeutung. *Feddes Repertorium* **80**, 463–590.

DAVIS, A. R., PETERSON, R. L. & SHUEL, R. W. (1986). Anatomy and vasculature of floral nectaries of *Brassica napus* (Brassicaceae). *Canadian Journal of Botany* **64**, 2508–2516.

DELPINO, F. (1868–75). Ulteriori osservazioni sulla dicogamia nel regno vegetale. I & II. *Atti della Societás Italiana di Scienze Naturali*, XI, XII.

DENISSOVA, G. A. (1975). Attempt at classification of terpenoid-containing conceptacles in plants. *Botanicheskii Zhurnal SSSR* **60**, 1698–1706. (In Russian).

DENISSOVA, G. A. (1976). Comparative study of the secretory vesicles in species of the genus *Dictamnus* (Rutaceae) in the flora of the USSR. *Rastitel'nye Resursy* **12**, 24–40. (In Russian)

DISTELBARTH, H. & KULL, U. (1985). Physiological investigations of leaf mucilages. II. The mucilage of *Taxus baccata* L. and of *Thuja occidentalis* L. *Israel Journal of Botany* **34**, 113–128.

DÜMMER, R. (1911). Grape sugar as a secretion in *Platycerium*. *Annals of Botany* **25**, 1205–1206.

DURKEE, L. T. (1982). The floral and extra-floral nectaries of *Passiflora*. II. The extra-floral nectary. *American Journal of Botany* **69**, 1420–1428.

DURKEE, L. T., GAAL, D. J. & REISNER, W. H. (1981). The floral and extra-floral nectaries of *Passiflora*. I. The floral nectary. *American Journal of Botany* **68**, 453–462.

ELEFTHERIOU, E. P. & HALL, J. L. (1983). The extra-floral nectaries of cotton. I. Fine structure of the secretory papillae. *Journal of Experimental Botany* **34**, 103–119.

ELIAS, T. S. & GELBAND, H. (1976). Morphology and anatomy of floral and extrafloral nectaries in *Campsis* (Bignoniaceae). *American Journal of Botany* **63**, 1349–1353.

ERIKSSON, M. (1977). The ultrastructure of the nectary of red clover (*Trifolium pratense*). *Journal of Apicultural Research* **16**, 184–193.

EYMÉ, J. (1966). Infrastructure des cellules nectarigènes de *Diplotaxis erucoides* D.C., *Helleborus niger* L. et *H. foetidus* L. *Comptes Rendus de l'Académie des Sciences (Paris)* Sér. D **262**, 1629–1632.

EYMÉ, J. (1967). Nouvelles observations sur l'infrastructure de tissues nectarigènes floraux. *Botaniste* **50**, 169–183.

FAHN, A. (1949). Studies in the ecology of nectar secretion. *Palestine Journal of Botany*, Jerusalem Series **4**, 207–224.

FAHN, A. (1952). On the structure of floral nectaries. *Botanical Gazette* **113**, 464–470.

FAHN, A. (1953). The topography of the nectary in the flower and its phylogenetical trend. *Phytomorphology* **3**, 424–426.

FAHN, A. (1979*a*). *Secretory Tissues in Plants*. Academic Press, London.

FAHN, A. (1979*b*). Ultrastructure of nectaries in relation to nectar secretion. *American Journal of Botany* **66**, 977–985.

FAHN, A. (1982). *Plant Anatomy*, 3rd edn. Pergamon Press, Oxford.

FAHN, A. (1987*a*). Extrafloral nectaries of *Sambucus niger* L. *Annals of Botany* **60**, 299–308.

FAHN, A. (1987*b*). Secretory tissues and factors influencing their development. *Phyton* (in press).

FAHN, A. & BENAYOUN, J. (1976). Ultrastructure of resin ducts in *Pinus halepensis*: development, possible sites of resin synthesis, and mode of its elimination from the protoplast. *Annals of Botany* **40**, 857–863.

FAHN, A. & BENOUAICHE, P. (1979). Ultrastructure, development and secretion in the nectary of banana flowers. *Annals of Botany* **44**, 85–93.

FAHN, A. & EVERT, R. F. (1974). Ultrastructure of the secretory ducts of *Rhus glabra* L. *American Journal of Botany* **61**, 1–14.

FAHN, A. & JOEL, D. (1977). Development of primary secretory ducts in the stem of *Mangifera indica* L. (Anacardiaceae). In: *Tropical Botany* (Ed. D. J. Mabberly & Chang Kiaw Lau), suppl. of *The Gardens' Bulletin, Singapore*, pp. 161–164.

FAHN, A. & RACHMILEVITZ, T. (1970). Ultrastructure and nectar secretion in *Lonicera japonica*. In: *New Research in Plant Anatomy* (Ed. by N. K. B. Robson, D. F. Cutler & M. Gregory). 51–56 pp. Academic Press, London.

FAHN, A. & RACHMILEVITZ, T. (1975). An autoradiological study of nectar secretion in *Lonicera japonica* Thunb. *Annals of Botany* **39**, 975–976.

FAHN, A. & SHIMONY, C. (1977). Development of glandular and non-glandular leaf hairs of *Avicennia marina* (Forskål) Vierh. *Botanical Journal of the Linnean Society* **74**, 37–46.

FAHN, A., WERKER, E. & BEN-ZUR, P. (1979). Seasonal effects of wounding and growth hormones on the development of traumatic ducts in *Cedrus libàni*. *New Phytologist* **82**, 537–544.

FAHN, A. & ZAMSKI, E. (1970). The influence of pressure, wind, wounding and growth substances on the rate of resin duct formation in *Pinus halepensis* wood. *Israel Journal of Botany* **19**, 429–446.

FAROOQUI, P. (1979–80). Structure and development of trichomes in *Eucalyptus torellina* F.v.M. *Phyta* **2** (3), 67–72.

FEHER, D. (1923). Über die Abscheidung von Harzbalsam und den jungen Trieben unserer einheimischen *Populus*-Arten. *Beihefte zum botanischen Zentralblatt* **39**, 81–103.

FIGDOR, W. (1891). Über die extranuptialen Nektarien von *Pteridium aquilinum*. *Österreichische botanische Zeitschrift* **41**, 293–295.

FIGIER, J. (1968). Localisation infrastructurale de la phosphomonoestérase acide dans la stipule de *Vicia faba* L. au niveau du nectaire. Rôles possibles de cet enzyme dans les mecanismes de la sécrétion. *Planta* **83**, 60–79.

FIGIER, J. (1971). Etude infrastructurale de la stipule de *Vicia faba* L. au niveau du nectaire. *Planta* **98**, 31–49.

FIGIER, J. (1972). Localisation infrastructurale de la phosphatase acide dans les glandes pétiolaires d'*Impatiens holstii*. Rôles possibles de cette enzyme au cours des processus sécrétoires. *Planta* **108**, 215–226.

FINDLAY, N. & MERCER, F. V. (1971). Nectar production in *Abutilon*. II. Submicroscopic structure of the nectary. *Australian Journal of Biology Sciences* **24**, 657–664.

FREI, E. (1955). Die Innervierung der floralen Nektarien dikotyler Pflanzenfamilien. *Berichte der schweizerischen botanischen Gesellschaft* **65**, 60–114.

FREY-WYSSLING, A. (1933) Über die extrafloralen Nektarien von *Hevea brasiliensis* Muell. *Berichte der schweizerischen botanischen Gesellschaft* **42**, 109–122.

FREY-WYSSLING, A. (1935). *Die Stoffausscheidung der höheren Pflanzen*. Springer, Berlin.

FREY-WYSSLING, A. (1955). The phloem supply to the nectaries. *Acta Botanica Neerlandica* **4**, 358–369.

FREY-WYSSLING, A. & AGTHE, C. (1950). Nektar ist ausgeschiedener Phloemsaft. *Verhandlungen der schweizerischen naturforschenden Gesellschaft* **130**, 175–176.

GEDALOVICH, E. & FAHN, A. (1985*a*). The development and ultrastructure of gum ducts in *Citrus* plants formed as a result of brown-rot gummosis. *Protoplasma* **127**, 73–81.

GEDALOVICH, E. & FAHN, A. (1985*b*). Ethylene and gum duct formation in *Citrus*. *Annals of Botany* **56**, 571–577.

GOODWIN, T. W. & MERCER, E. I. (1972). *Introduction to Plant Biochemistry*. Pergamon Press, Oxford.

GROOM, P. (1926). Excretory systems in secondary xylem of Meliaceae. *Annals of Botany* **40**, 633–649.

GROSCLAUDE, C. (1966). La gommose des arbres fruitiers. *Annales des Epiphyties* **17**, 129–137.

GUNNING, B. E. S. & HUGHES, J. E. (1976). Quantitative assessment of symplastic transport of pre-nectar into the trichomes of *Abutilon* nectaries. *Australian Journal of Plant Physiology* **3**, 619–637.

GUTTERMAN, Y., WHITZTUM, A. & EVENARI, M. (1967). Seed dispersal and germination in *Blepharis persica* (Burm.) Kunze. *Israel Journal of Botany* **16**, 213–234.

HABERLANDT, G. (1886). Zur Anatomie und Physiologie der pflanzlichen Brennhaare. *Sitzungsberichte der Akademie der Wissenschaften in Wien* **93**, 122–145.

HABERLANDT, G. (1894). Über Bau und Funktion der Hydathoden. *Berichte der deutschen botanischen Gesellschaft* **12**, 367–378.

HABERLANDT, G. (1918). *Physiologische Pflanzenanatomie*, 5th edn. Engelmann, Leipzig.

HEINRICH, G. (1975*a*). Über die Lokalisation verschiedener Phosphatase im Nektarium von *Aloë*. *Cytobiologie* **11**, 247–263.

HEINRICH, G. (1975*b*). Über den Glucose-Metabolismus in Nektarien zweier *Aloë*-Arten und über den Mechanismus der Pronektar-Sekretion. *Protoplasma* **85**, 351–371.

HEINRICH, G. & SCHULTZE, W. (1985). Composition and site of biosynthesis of the essential oil in fruits of *Phellodendron amurense* Rupr. (Rutaceae). *Israel Journal of Botany* **34**, 205–217.

HILL, A. E. & HILL, B. S. (1976). Elimination processes by glands. Mineral ions. In: *Encyclopedia of Plant Physiology*, new series, vol. 2. *Transport in Plants*, II B (Ed. by U. Lüttge & M. G. Pitman), pp. 225–243. Springer, Berlin.

HORNER, H. T. JR & LERSTEN, N. R. (1968). Development, structure and function of secretory trichomes in *Psychotria bacteriophila* (Rubiaceae). *American Journal of Botany* **55**, 1089–1099.

HUURRE, A., HUHTIKAGAS, S. & WIDEN, C.-J. (1979). Electron microscopic investigations on internal glandular hairs of *Dryopteris* ferns. *Planta Medica* **35**, 262–269.

IMASEKI, H., YOSHII, H. & TODAKA, I. (1982). Regulation of auxin-induced ethylene biosynthesis in plants. In: *Plant Growth Substances* (Ed. by P. F. Wareing), pp. 259–268. Academic Press, London.

JAIN, K. K. (1976). Evolution of wood structure in Pinaceae. *Israel Journal of Botany* **25**, 28–33.

JOEL, D. M. & FAHN, A. (1980*a*). Ultrastructure of resin ducts of *Mangifera indica* L. (Anacardiaceae). 1. Differentiation and senescence of the shoot ducts. *Annals of Botany* **46**, 225–233.

JOEL, D. M. & FAHN, A. (1980*b*). Ultrastructure of resin ducts of *Mangifera indica* L. (Anacardiaceae). 2. Resin secretion in the primary stem ducts. *Annals of Botany* **46**, 779–783.

Joel, D. M. & Fahn, A. (1980*c*). Ultrastructure of resin ducts of *Mangifera indica* L. (Anacardiaceae). 3. Secretion of protein–polysaccharide mucilage in the fruit. *Annals of Botany* **46**, 785–790.

Jones, J. F. & Lende, H. (1979). Auxin-induced ethylene biosynthesis in subapical stem sections of etiolated seedlings of *Pisum sativum* L. *Planta* **146**, 649–656.

Kalman, F. & Gulyás, S. (1974). Ultrastructure and mechanism of secretion in extrafloral nectaries of *Ricinus communis* L. *Acta Biologica Szeged* **20**, 57–67.

Kartashova, N. N. (1965). *Stroeniei Funktsiya Nektarnikov Tsvetka dvudol'nykh rastenii*. Izdatel'stvo Tomskogo Universiteta. Tomsk.

Keeler, K. H. & Kaul, R. B. (1984). Distribution of defense nectaries in *Ipomoea* (Convolvulaceae). *American Journal of Botany* **71**, 1364–1372.

Kisser, J. (1958). Der Stoffwechsel sekundärer Pflanzenstoffe. In: *Handbuch der Pflanzenphysiologie*, vol. 10 (Ed. by W. Ruhland), pp. 91–131. Springer, Berlin.

Kristen, U. (1976). Die Morphologie der Schleimsekretion in Fruchtknoten von *Aptenia cordifolia*. *Protoplasma* **89**, 221–233.

Kristen, U. & Lockhausen, J. (1985). The leaf glands of *Veronica beccabunga* L.: ultrastructure and a possible pathway of secretion. *Israel Journal of Botany* **34**, 147–156.

Kronestedt, E. C., Robards, A. W., Stark, M. & Olsen, P. (1986). Development of trichomes in the *Abutilon* nectary gland. *Nordic Journal of Botany* **6**, 627–639.

Leemann, A. (1928). Das Problem der Sekretzellen. *Planta* **6**, 216–233

Lehmann, C. (1926). Studien über den Bau und die Entwicklungsgeschichte von Ölzellen. *Planta* **1**, 343–373.

Lersten, N. R. (1975). Colleter types in Rubiaceae, especially in relation to the bacterial leaf nodule symbiosis. *Botanical Journal of the Linnean Society* **71**, 311–319.

Levering, C. A. & Thomson, W. W. (1971). The ultrastructure of the salt gland of *Spartina foliosa*. *Planta* **97**, 183–196.

Levering, C. A. & Thomson, W. W. (1972). Studies of the ultrastructure and mechanism of secretion of the salt gland of the grass *Spartina*. *Proceedings of the 30th Electron Microscopy Society of America* **22**, 223.

Levin, D. A. (1973). The role of trichomes in plant defense. *Quarterly Review of Biology* **48**, 3–15.

Liphshitz, N., Shomer-Ilan, A., Eshel, A. & Waisel, Y. (1974). Salt glands on leaves of rhodes grass (*Chloris gayana* Kth.). *Annals of Botany* **38**, 459–462.

Liphshitz, N. & Waisel, Y. (1974). Existence of salt glands in various genera of the Gramineae. *New Phytologist* **73**, 507–513.

Lüttge, U. (1961). Über die Zusammensetzung des Nektars und den Mechanismus seiner Sekretion. I. *Planta* **56**, 189–212.

Lüttge, U. (1969). Aktiver Transport (Kurzstreckentransport bei Pflanzen). *Protoplasmatologia* **8**, 1–146.

Lüttge, U. (1971). Structure and function of plant glands. *Annual Review of Plant Physiology* **22**, 23–44.

Lüttge, U. (1977). Nectar composition and membrane transport of sugars and amino acids. A review on the present state of nectar research. *Apidologie* **8**, 305–320.

Lüttge, U. & Schnepf, E. (1976). Elimination processes by glands. Organic substances. In: *Transport in Plants*, II. *Encyclopedia of Plant Physiology*. N.S. vol. 2, part B (Ed. U. Lüttge & M. G. Pitman), pp. 244–277. Springer, Berlin.

Magin, N. (1983). Die Nektarien der Apiaceae. *Flora* **173**, 233–254.

Mahlberg, P. G., Hammond, C. T., Turner, J. C. & Hemphill, J. K. (1984). Structure, development and composition of glandular trichomes of *Cannabis sativa* L. In: *Biology and Chemistry of Plant Trichomes* (Ed. by E. Rodriguez, P. L. Healey & I. Mehta), pp. 23–51. Plenum Press, New York and London.

Marginson, R., Sedgley, M. & Knox, R. B. (1985*a*). Structure and histochemistry of the extrafloral nectary of *Acacia terminalis* (Salisb.) MacBride (Leguminosae, Mimosoideae). *Protoplasma* **127**, 21–30.

Marginson, R., Sedgley, M., Douglas, T. J. & Knox, R. B. (1985*b*). Structure and secretion of the extrafloral nectaries of Australian acacias. *Israel Journal of Botany* **34**, 91–102.

Maron, R. & Fahn, A. (1979). Ultrastructure and development of oil cells in *Laurus nobilis* L. leaves. *Botanical Journal of the Linnean Society* **78**, 31–40.

Matile, Ph. (1956). Über den Stofwechsel und die Auxinabhängigkeit der Nektarsekretion. *Berichte der schweizerischen botanischen Gesellschaft* **66**, 237–266.

Meeuse, A. D. J. (1978). Nactarial secretion, floral evolution, and pollination syndrome in early angiosperms. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam*, Ser. C **81**, 300–326.

Metcalfe, C. R. (1967). Distribution of latex in the plant kingdom. *Economic Botany* **21**, 115–125.

Metcalfe, C. R. & Chalk, L. (1983). *Anatomy of the Dicotyledons*, 2nd edn, vol. II, *Wood structure and Conclusion of the General Introduction*. Clarendon Press, Oxford.

Meyberg, M. & Kristen, U. (1981). The nectaries *Aptenia cordifolia*. Ultrastructure, translocation of ^{14}C-labelled sugars, and a possible pathway of secretion. *Zeitschrift für Pflanzenphysiologie* **104**, 139–147.

Mikulska, E. & Zolnierowicz, H. (1976). Ultrastructure of plastids in differentiating epithelial cells of *Abies homolepis* Sib. and Zucc. leaves. *Biochemie und Physiologie der Pflanzen* **170**, 355–362.

Mohan, J. S. S. & Inamdar, J. A. (1986). Ultrastructure and secretion of extrafloral nectaries of *Plumeria rubra* L. *Annals of Botany* **57**, 389–401.

Moréou, M., Catesson, A. M., Peresse, M. & Czaninski, Y. (1978). Dynamique comparée des réactions cytologiques du xylème de l'oeillet en présence de parasites vasculaires. *Phytopathologische Zeitschrift* **91**, 289–306.

MORRISON, J. C. & POLITO, V. S. (1985). Gum duct development in almond fruit, *Prunus dulcis* (Mill.) D. A. Webb. *Botanical Gazette* **146**, 15–25.

MÜLLER, N. J. C. (1866–1867). Untersuchungen über die Verteilung der Harze, ätherischen Öle, Gummi und Gummiharze, und die Stellung der Sekretionsbehälter in Pflanzenkörper. *Jahrbüch für wissenschaftliche Botanik* **5**, 387–421.

NAPP-ZINN, K. (1966). *Anatomie des Blattes. I. Blattanatomie der Gymnospermen.* In: *Handbuch der Pflanzenanotomie*, Bd 8, Teil 1 (Ed. by W. Zimmermann, P. Ozenda & H. D. Wulff). Borntraeger Berlin.

OGURA, Y. (1972). *Comparative Anatomy of Vegetative Organs of the Pteridophytes.* 2nd end. In: *Handbuch der Pflanzenanatomie*, Bd. 7, Teil 3 (Ed. by K. Linsbauer), Borntraeger, Berlin.

OSMOND, C. B., LÜTTGE, U., WEST, K. R., PALLAGHY, C. K. & SHACHAR-HILL, B. (1969). Ion absorption in *Atriplex* leaf tissue. II. Secretion of ions to epidermal bladders. *Australian Journal of Biological Sciences* **22**, 797–814.

PAECH, K. (1952). Die Differenzierung der Ölzellen und die Bildung des ätherischen Öles bei *Asarum europaeum*. *Zeitschrift für Botanik* **40**, 53–66.

PATE, J. S. & GUNNING, B. E. S. (1972). Transfer cells. *Annual Review of Plant Physiology* **123**, 173–196.

PENHALLOW, D. P. (1907). *A Manual of the North American Gymnosperms*. Ginn, Boston.

PERCIVAL, M. S. (1961). Types of nectar in angiosperms. *New Phytologist* **60**, 235–281.

PEREIRA DA COSTA, T. G. C. A. (1985). *Bolsas secretoras de* Ruta chalepensis *L.* Ph.D. thesis of the University of Lisbon.

PRIDGEON, A. M. & STERN, W. L. (1983). Ultrastructure of osmophores in *Restrepia* (Orchidaceae). *American Journal of Botany* **70**, 1233–1243.

RACHMILEVITZ, T. & FAHN, A. (1973). Ultrastructure of nectaries of *Vinca rosea* L., *Vinca major* L. and *Citrus sinensis* Osbeck cv. *Valencia* and its relation to the mechanism of nectar secretion. *Annals of Botany* **37**, 1–9.

RACHMILEVITZ, T. & FAHN, A. (1975). The floral nectary of *Tropaeolum majus* L.—The nature of the secretory cells and the manner of nectar secretion. *Annals of Botany* **39**, 721–728.

RACHMILEVITZ, T. & JOEL, D. M. (1976). Ultrastructure of the calyx glands of *Plumbago capensis* Thunb. in relation to the process of secretion. *Israel Journal of Botany* **25**, 127–139.

REED, M. L., FINDLAY, N. & MERCER, F. V. (1971). Nectar production in *Abutilon*. IV. Water and solute relations. *Australian Journal of Biological Sciences* **24**, 677–688.

RICKARD, J. E. & GAHAN, P. B. (1983). The development of occlusions in cassava (*Manihot esculenta* Crantz) root xylem vessels. *Annals of Botany* **52**, 811–821.

ROUGIER, M. (1972). Etude cytochimique des squamules d'*Elodea canadensis*. Mise en évidence de leur sécrétion polysaccharidique et de leur activité phosphatasique acide. *Protoplasma* **74**, 113–131.

ROUGIER, M. & CHABOUD, A. (1985). Mucilages secreted by roots and their biological function. *Israel Journal of Botany* **34**, 129–146.

SAID, C. (1982). Les nectaires floraux des Crassulacées. Etude morphologique, histologique et anatomique. *Bulletin de la Société Botanique de France* **129**, 231–240.

SCHEMSKE, D. W. (1980). The evolutionary significance of extrafloral nectar production by *Costus woodsonii* (Zingiberaceae), an experimental analysis of ant protection. *Journal of Ecology* **68**, 959–967.

SCHNEPF, E. (1964). Zur Cytologie und Physiologie pflanzlicher Drüsen. 4. Teil. Licht- und elektronenmikroskopische Untersuchungen an Septalnektarien. *Protoplasma* **58**, 137–171.

SCHNEPF, E. (1968). Zur Feinstruktur der schleimsezernierenden Drüsenhaare auf der Ochrea von *Rumex* and *Rheum*. *Planta* **79**, 22–34.

SCHNEPF, E. (1969*a*). *Sekretion und Exkretion bei Pflanzen. Protoplasmatologia* VIII/8. Springer, Vienna and New York.

SCHNEPF, E. (1969*b*). Über den Feinbau von Öldresen, IV. Die Ölgenge von Umbelliferen: *Heracleum sphondylium* und *Dorema ammoniacum*. *Protoplasma* **67**, 375–390.

SCHNEPF, E. (1972). Tubuläres endoplasmatisches Reticulum in Drüsen mit lipophilen Ausscheidungen von *Ficus*, *Ledum* und *Salvia*. *Biochemie und Physiologie der Pflanzen* **163**, 113–125.

SCHNEPF, E. & CHRIST, P. (1980). Unusual transfer cells in the epithelium of the nectaries of *Asclepias curassavica* L. *Protoplasma* **105**, 135–148.

SCHNEPF, E. & DEICHGRÄBER, G. (1984). Electron microscopical studies of nectaries of some *Euphorbia* species. *Akademie der Wissenschaften und der Literatur. Mainz, Mathematisch-Naturwissenschaftlichen Klasse, Tropische und subtropische Pflanzenwelt* **45**, 55–93.

SCHNEPF, E., DEICHGRÄBER, G. & BARTHLOTT, W. (1983). On the fine strucutre of the liquid producing floral gland of the orchid, *Coryanthes speciosa*. *Nordic Journal of Botany* **3**, 479–491.

SCHRÖDTER, K. (1926). Zur physiologischen Anatomie der Mittelzelle drüsiger Gebilde. *Flora* **120**, 19–86.

SHAH, J. J. & BABU, A. M. (1986). Vascular occlusions in stem of *Ailanthus excelsa* Roxb. *Annals of Botany* **57**, 603–611.

SHIMONY, C. & FAHN, A. (1968). Light- and electron-microscopical studies on the structure of salt glands of *Tamarix aphylla* L. *Botanical Journal of the Linnean Society* **60**, 283–288.

SHIMONY, C., FAHN, A. & REINHOLD, L. (1973). Ultrastructure and ion gradients in the salt glands of *Avicennia marina* (Forsk.) Vierh. *New Phytologist* **72**, 27–36.

SHUEL, R. W. (1961). Influence of reproductive organs on secretion of sugar in flowers of *Streptosolen jamesonii*. *Plant Physiology* **36**, 265–271.

Skelding, A. P. & Winterbotham, J. (1939). The structure and development of hydathodes of *Spartina townsendii* Groves. *New Phytologist* **38**, 69–79.

Smets, E. (1986). Localization and systematic importance of the floral nectaries in the Magnoliaceae (Dicotyledons). *Bulleting du Jardin Botanique National de Belgique* **56**, 51–76.

Smith, B. N. & Meeuse, B. J. (1966). Production of volatile amines and skatole at anthesis in some *Arum* lily species. *Plant Physiology* **41**, 343–347

Sperlich, A. (1939). *Exkretionsgewebe*. In: *Handbuch der Pflanzenanatomie*, vol. 4, *Das tropische Parenchym*. (Ed. by K. Linsbauer). Borntraeger, Berlin.

Stösser, R. (1979). Investigations on gum duct formation in cherries using plastic embedding medium. *Scientia Horticulturae* **11**, 247–252.

Sutherland, G. H. & Eastwood, A. (1916). The physiological anatomy of *Spartina townsendii*. *Annals of Botany* **30**, 333–351.

Tăcină, F. (1973). La structure optique et électronmicroscopique de la glande nectarifère chez *Cynoglossum officinale* L. *Revue Roumaine de Biologie, Série de Botanique* **18**, 201–209.

Tarkowska, J. A., Zobel, A. M. & Maciak, M. (1981). Development and transfer character of secretory glands in the broad bean (*Vicia faba* L.). *Acta Societatis Botanicorum Poloniae* **50**, 391–398.

Thomson, W. W. (1975). The structure and function of salt glands. In: *Plants in Saline Environments* (Ed. by A. Poljakoff-Mayber and J. Gale), pp. 118–146. Springer, Berlin.

Thomson, W. W. & Healey, P. L. (1984). Cellular basis of trichome secretion. In: *Biology and Chemistry of Plant Trichomes* (Ed. by E. Rodriguez, P. L. Healey & I. Mehta), pp. 95–111. Plenum, New York and London.

Thomson, W. W. & Liu, L. L. (1967). Ultrastructural features of the salt gland of *Tamarix aphylla*. *Planta* **73**, 201–220.

Thomson, W. W., Berry, W. L. & Liu, L. L. (1969). Localization and secretion of salt by the salt glands of *Tamarix aphylla*. *Proceedings of the National Academy of Sciences of the U.S.A.* **63**, 310–317.

Thomson, W. & Platt-Aloia, K. (1979). Ultrastructural transitions associated with the development of the bladder cells of the trichomes of *Atriplex*, *Cytobios* **25**, 105–114.

Thurston, E. L. & Lersten, N. R. (1969). The morphology and toxicology of plant stinging hairs. *The Botanical Review* **35**, 393–412.

Trachtenberg, S. & Fahn, A. (1981). The mucilage cells of *Opuntia ficus-indica* (L) Mill: development, ultrastructure, and mucilage secretion. *Botanical Gazette* **142**, 206–213.

Tschirch, A. (1889). *Angewandte Pflanzenanatomie*. Urban und Schwarzberg, Vienna.

Tschirch, A. (1906). *Die Harze und die Harzbehälter mit Einschluss der Milchsafte*, 2. Aufl. Leipzig.

Tucker, S. C. (1976). Intrusive growth of secretory oil cells in *Saururus cernuus*. *Botanical Gazette* **137**, 341–347.

Unzelman, J. M. & Healey, P. T. (1974). Development, structure and occurrence of secretory trichomes of *Pharbitis*. *Protoplasma* **80**, 285–303.

Uphof, J. C. Th. (1962). *Plant Hairs*. In: *Handbuch der Pflanzenanatomie*, Bd. 4, Teil 5 (Ed. by K. Linsbauer). Borntraeger, Berlin.

Vander Molen, G. E., Beckman, C. H. & Rodehorst, E. (1977). Vascular gelation, a general response phenomenon following infection. *Physiological Plant Pathology* **11**, 95–100

Van Steveninck, R. F. M., Armstrong, W. D., Peters, P. D. & Hall, T. A. (1976). Ultrastructural localization of ions. III. Distribution of chloride in mesophyll cells of mangrove (*Aegiceras corniculatum* Blanco). *Australian Journal of Plant Physiology* **3**, 367–376.

Vassilyev, A. E. (1969). Submicroscopic morphology of nectary cells and problems of nectar secretion. *Botanicheskii Zhurnal SSSR* **54**, 1015–1031. (In Russian)

Vassilyev, A. E. (1970). On the localization of terpenoids synthesis in plant cells. *Rastitel'nye Resursy* **6**, 29–45. (In Russian)

Vassilyev, A. E. (1971). New data on the ultrastructure of the cells of flower nectary. *Botanicheskii Zhurnal SSSR* **56**, 1292–1306. (In Russian)

Vassilyev, A. E. (1977). *Functional Morphology of Plant Secretory Cells*. Nauka, Leningrad. (In Russian)

Vermeer, J. & Peterson, R. L. (1979). Glandular trichomes on the inflorescence of *Chrysanthemum morifolium* cv. Dramatic (Compositae). II. Ultrastructure and histochemistry. *Canadian Journal of Botany* **57**, 714–729.

Vogel, S. (1962). Duftdrüsen im Dienst der Bestaübung. Über Bau und Funktion der Osmophoren. *Akademie der Wissenschaften und der Literatur, Mainz, Abhandlung der Mathematisch-Naturwissenschaftliche* Klasse **10**, 598–763.

Vogel, S. (1966). Scent organs of flowers and their relation to insect pollination. In: *Proceedings of the 5th World Orchid Conference* (Ed. by L. R. DeGarmo), pp. 253–259. Long Beach, CAL, U.S.A.

Vogel, S. (1981). Trichomnatische Blütennektarien bei Cucurbitaceen. *Beiträge zur Biologie der Pflanzen* **55**, 325–353.

Walter, H. & Steiner, M. (1937). Die Okolgie der Ost-Afrikanischen Mangroven. *Zeitschrift für Botanik* **30**, 65–193.

Wergin, P. W., Elmore, C. D., Hanny, B. W. & Ingber, B. (1975). Ultrastructure of the subglandular cells from the foliar nectaries of cotton in relation to the distribution of plasmodesmata and symplastic transport of nectar. *American Journal of Botany* **62**, 842–849.

Werker, E. & Fahn, A. (1969). Resin ducts of *Pinus halepensis* Mill.—Their structure, development and pattern of arrangement. *Botanical Journal of the Linnean Society* **62**, 379–411.

WERKER, E. & FAHN, A. (1981). Secretory hairs of *Inula viscosa* (L.) Ait.: development, ultrastructure, and secretion. *Botanical Gazette* **142**, 461–476.

WERKER, E. & KISLEV, M. (1978). Mucilage on the root surface and root hairs of *Sorghum*: heterogeneity in structure, manner of production and site of accumulation. *Annals of Botany* **42**, 809–816.

WERKER, E., RAVID, U. & PUTIEVSKY, E. (1985*a*). Structure of glandular hairs and identification of the main components of their secreted material in some species of the Labiatae. *Israel Journal of Botany* **34**, 31–45.

WERKER, E., RAVID, U. & PUTIEVSKY, E. (1985*b*). Glandular hairs and their secretions in the vegetative and reproductive organs of *Salvia sclarea* and *S. dominica*. *Israel Journal of Botany* **34**, 239–252.

WHATLEY, J. M. & WHATLEY, F. R. (1987). When is a chromoplast? *New Phytologist* **106**, 667–678.

WIDEN, C.-J. & BRITTON, D. M. (1969). A chromatographic and cytological study of *Dryopteris dilatata* in eastern North America. *Canadian Journal of Botany* **47**, 1337–1344

WOLLENWEBER, E. (1984). The systematic implication of flavonoids secreted by plants. In: *Biology and Chemistry of Plant Trichomes* (Ed. by E. Rodriguez, P. L. Healey & I. Mehta). Plenum, New York and London.

YAMAMOTO, F. & KOZLOWSKI, T. T. (1987*a*). Effect of ethrel on growth and stem anatomy of *Pinus halepensis* seedlings. *IAWA Bulletin* **8**, 11–19.

YAMAMOTO, F. & KOZLOWSKI, T. T. (1987*b*). Effect of flooding, tilting of stem and ethrel application on growth, stem anatomy and ethylene production of *Pinus densiflora* seedlings. *Journal of Experimental Botany* **38**, 293–310

YAMAMOTO, F., KOZLOWSKI, T. T. & WOLTER, K. E. (1987). Effect of flooding on growth, stem anatomy, and ethylene production of *Pinus halepensis* seedlings. *Canadian Journal of Forest Research* **17**, 69–79.

YANG, S. F., ADAMS, D. O., LIZADA, C., YU, Y., BRADFORD, K. J., CAMERON, A. C. & HOFFMAN, N. E. (1980). Mechanism of ethylene biosynthesis. In: *Plant Growth Substances* (Ed. by F. Skoog), pp. 219–229. Springer, Berlin.

ZANDONELLA, P. & PIOLAT, C. (1982). Nectaires et sécrétion du nectar chez *Thunbergia laurifolia* Lindl. (Acanthacées). *Bulletin de la Société botanique de France* **129**, 109–117.

ZIEGLER, A. (1960). Zur Anatomie und Protoplasmatik der Ölidioblasten von *Houttuynia cordata*. *Protoplasma* **51**, 539–562.

ZIEGLER, H. (1965). Die Physiologie pflanzlicher Drüsen. *Berichte der deutschen botanischen Gesellschaft* **78**, 466–477.

ZIEGLER, H. & LÜTTGE, U. (1959). Über die Resorption von C^{14}-Glutaminsäure durch sezernierende Nektarien. *Naturwissenschaften* **46**, 176–177.

ZIMMERMANN, J. G. (1932). Über die extrafloralen Nektarien der Angiospermen. *Beihefte zum botanischen Zentralblatt* **49** A, 99–196.

ZIMMERMANN, M. (1953). Papierchromatographische Untersuchungen über die pflanzliche Zuckersekretion. *Berichte der schweizerischen botanischen Gesellschaft* **63**, 402–429.