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Review

Secreting Glandular Trichomes: More than Just Hairs

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ABSTRACT

Secreting glandular plant trichome types which accumulate large quantities of metabolic products in the space between their gland cell walls and cuticle permit the plant to amass secretions in a compartment that is virtually outside the plant body. These structures not only accumulate and store what are often phytotoxic oils but they position these compounds as an apparent first line of defense at the surface of the plant. Recent advances in methods for isolation and study of trichome glands have allowed more precise analysis of gland cell metabolism and enzymology. Isolation of mutants with altered trichome phenotypes provides new systems for probing the genetic basis of trichome development. These advances and their continuation can pave the way for future attempts at modification of trichome secretion. The biochemical capability of glandular secreting trichomes and the potential for its future manipulation to exploit this external storage compartment is the focus of this review.

Most surfaces of most plants are said to be pubescent, or bearing of trichomes or hairs. The morphology of these structures can vary greatly with tissue and species. Indeed, the botanical literature is said to contain more than 300 descriptions (uniseriate, capitate-sessile, etc.) to characterize various morphological types (see Benhnke, 22). These characteristics have often been used in plant classification. Functionally, trichomes may be simple hairs which deter herbivores, guide the path of pollinators or affect photosynthesis, leaf temperature, or water loss through increased light reflectance as in desert species (see Kelsey *et al.*, 22). Or, they may be more specialized tissues (glandular secreting trichomes) whose principal function(s) may be to produce pest- or pollinator-interactive chemicals which are stored or volatilized at the plant surface. It has been suggested that in some desert species the principal role of glandular secreting trichomes is to produce such high levels of exudate that it forms a continuous layer on the plant surface. This layer may increase light reflectance and thereby reduce leaf temperature (4).

It is the glandular, merocrine, secreting trichome type which often produce and accumulate terpenoid oils that will be the focus of this paper. Other secretory tissues occurring on or in plants including salt glands, salt hairs, nectary and slime glands, resin ducts, and osmophores (often responsible for fragrances in flowers) will not be included in this discussion. Comprehensive reviews which consider various secretory tissues of plants are found in references 4, 6, 19, and 22. We will argue here that glandular secreting trichomes are an attractive system for study and are now or will soon be amenable to modification using a recombinant DNA approach. Useful modification might be genetic manipulation of an enzyme to alter the chemical nature of exudate for the purpose of enhancing disease resistance, enhancing attractiveness to pollinators, or to expand the metabolism of secretory cells to include synthesis of compounds or intermediates not normally formed. It is important to point out here that the potential of secreting trichomes to accumulate exudate is highly significant in certain plants where, under optimal conditions, secreted products can reach a level of 10 to 30% of the dry weight of leaves (4, and Kelsey *et al.*, 22). Glandular trichome exudates usually contain terpenes and essential oils (4), lipophilic components not easily stored in large amounts within the cell. Therefore, if it were desirable to manipulate plants to produce or overproduce a compound in this class of biochemicals, the secreting trichome system which amasses secretions outside of gland cells may be more amenable to overproduction than one requiring intracellular storage.

This minireview will first consider some general aspects of trichome biology with emphasis on recent work concerning the molecular basis of trichome and root hair development. This will be followed by sections which consider our present understanding of which tissues form secretions, how structure and ultrastructure relate to the potential to amass secretions, and which metabolic pathways are known to occur in secretory cells. A brief "one physiologist's view" of aspects of plant-insect, plant-microbe interactions will follow and the last section will consider some possibilities for future studies and manipulation of trichome secretion.

GENERAL ASPECTS OF PLANT TRICHOMES

Esau (5) has defined trichomes as "epidermal appendages of diverse form, structure and functions. . . . represented by protective, supporting, and glandular hairs, by scales, by various papillae, and by absorbing hairs of roots." This definition suggests a close relationship between trichomes and root hairs. From this viewpoint, aerial trichomes and subterranean "trichomes" could be said to cover or nearly cover the surfaces of most plants. However, recent results would suggest that while trichomes and root hairs may resemble each other in morphology, their genetic determinants may differ (see below). Both trichomes and root hairs develop as projections from protodermal cells. Glandular structures of trichomes arise from a series of anticlinal and periclinal divisions to

form supporting auxiliary cells and glands as in the case of *Cannabis* (see Mahlberg *et al.*, 22).

Some recent work promises to shed light on the molecular genetic basis of trichome development. Mutants of *Arabidopsis* have been isolated in which phenotypic changes are limited to trichomes (11, 18). The absence of trichomes in mutants gl1 and ttg1 does not affect overall plant growth and development to the extent that this has been tested. It is probable that these loci are the only ones associated with the loss of trichomes in *Arabidopsis* because a number of independently isolated mutants failed to complement these two loci (18). Thus, these genes appear to be responsible for differentiation of protodermal cells to form trichomes. Trichomeless mutants of *Arabdopsis* form normal root hairs suggesting, as noted above, that different genes control formation of trichomes and root hairs (C Somerville, personal communication). Noteworthy is the observation that trichomes are often the earliest recognizable structures to appear during differentiation of cultured tissue. Perhaps this reflects the linkage of trichome-determining genes and other genes involved in early development. The study of the structure and regulation of trichome genes, such as the recent work of Herman and Marks with *Arabidopsis* (12), may serve to better define the genetic mechanisms of differentiation in plants and perhaps make possible alteration of trichome density to study the physiological roles of trichomes in, for example, light reflectance. Trichome structural and hairless mutants have been characterized at the morphological level in other plants, including tomato (21).

Genes affecting the formation of root hairs were also recently identified in *Arabidopsis* (23). Four classes of mutants all resulting from single nuclear recessive mutations were attributed to four different genes. One of these, RHD1, appears to be responsible for normal initiation of hairs while the others are involved in normal elongation. Hairy root cultures (24) which often, but not always, proliferate adventitious hairs and *Arabidopsis* mutants should provide useful systems for studying gene-level aspects of root hair development.

Much of what we know about the tissue and cell level sites and mechanisms of trichome secretion has come from cytochemical and ultrastructural studies (6). The recent development of a method for preparing protoplasts from root hairs (1) may facilitate characterization of enzymes and organelles of these cells. There is a great need for development of methods for preparing organelles from trichome secretory cells or protoplasts which could serve as a source of isolated organelles. Such preparations would be useful, for example, in studying the apparent intimate relationship between plastids and ER which appears to be so common in terpene secreting glands (6). We note that we have been unsuccessful thus far in attempts to prepare protoplasts from tobacco trichome glands applying protocols used for easily protoplasted or recalcitrant tissues. The difficulty may be the presence of modified cell walls and wall encrustations which are common in secreting glands (see Peterson and Vermer, 22).

WHICH TRICHOME CELLS FORM SECRETIONS AND WHAT IS THE EXTENT OF THEIR METABOLIC INDEPENDENCE?

The preceding discussion and much of the literature on trichomes has assumed that glandular cells of glandular trichomes produce secretions. The appearance of glands atop supporting cells and the occurrence of exudate around gland cells has suggested to most observers that secretions are produced in gland cells and not by other epidermal or subepidermal cells. This notion has been supported in a number of cases by cytochemical evidence showing accumulation of lypophilic materials within secreting gland cells (4, 6). However, proof that gland cells form exudate was only shown directly when quantities of highly purified glands prepared from tobacco (17) were shown to be capable of relatively efficient, light-dependent diterpene and sucrose ester synthesis from as simple a precursor as carbonate (13). Neither epidermal peels prepared from tissues brushed to remove glands (but not entire trichome stalks) nor pieces of subepidermal tissue synthesized these complex components while peels bearing glands were biosynthetically competent. Croteau and coworkers have recently isolated trichome glands from *Mentha*. While these glands—which are more difficult to obtain than glands of tobacco trichomes that have a longer stalk—show only limited potential for biosynthesis, they have been expertly exploited for isolation and localization of enzymes specific to monoterpene synthesis (7, 8). The studies with mint provide strong, indirect evidence that trichome glands of this plant synthesize and accumulate monoterpenes. Thus, there is now substantial evidence that monoterpenes and diterpenes (also sucrose esters) are produced within gland cells of secreting trichomes.

The finding that isolated secreting glands of tobacco can convert radiolabel from carbonate to complex diterpenes and to both the sucrose and acyl moieties of sucrose esters suggests that in tobacco, photosynthetically competent gland cells perhaps need only be supplied carbonate (13). Alternatively, sucrose or glucose may be supplied from subepidermis via highly vacuolated, chloroplast-less stalk cells. In favor of the former hypothesis is the finding that carbonate was a better donor of carbon to principal exudate constituents in gland cells of tobacco than were glucose or sucrose. Gaseous $^{14}CO_2$ was incorporated by epidermal peels having intact glands but not by detached glands. Studies using asymmetrically labeled sucrose (^{14}C-Glu-Fru) showed that both epidermal peels bearing secreting trichomes and isolated gland cell preparations randomized label before its incorporation into the sucrose moiety of sucrose esters (13). Thus, at least the secreting gland cells of tobacco appear to be metabolically independent in the light in producing principal exudate components if supplied carbonate. These cells contain numerous fully developed chloroplasts (20). Despite this compelling evidence for metabolic independence, we point out that sustained biosynthesis in isolated glands of tobacco has not been demonstrated. Further study is needed to determine if exudate formation is regulated by the supply of CO_2 or sugar in tobacco and other systems. It has been suggested that in mint, availability of assimilate to cells and cellular compartmentation involved in biosynthesis may regulate the rate of monoterpene synthesis (8).

IS EXUDATE ACCUMULATION CAPACITY RELATED TO THE STRUCTURE OF SECRETING CELLS?

In the following discussion, potential for amassing high levels of exudate is emphasized because this aspect may be

important in selecting plant systems to modify for potential commercial exploitation of trichome exudation or for efficient experimentation to modify pest-interactive properties of exudate. Great diversity exists in the morphology of glandular trichomes at the organ, cellular, and subcellular levels (6). This diversity occurs in plants which are lower-level accumulators (<2% of dry weight of leaves as exudate) and also in those which are high level accumulators (~5–30% dry weight of leaves). Many high level accumulators such as certain species of *Beyeria, Eromophilia, Lycopersicon, Solanum,* and *Nicotiana* appear to contain "bright green" chloroplasts (4) in secreting or auxiliary cells suggesting a possible relationship between their capacity to amass exudate and their photosynthetic capacity to fix carbon and/or to produce ATP and NADPH. However, at least one exception to this rule is found in *Newcastelia.* But, glands of this plant contain a type of plastid and also have exceptional ability to incorporate precursors into terpenes with unusually high rates as compared to most other higher terpene and also monoterpene producers (4). Further study comparing high and lower level secreting plants is needed to determine if gland photosynthetic potential and capacity to secrete are related. Generally, high-level exudate accumulators produce di-, tri-, and sesquiterpenes as major products. Plants which principally form monoterpenes commonly amass lower levels of exudate but the generally higher volatility of these lower terpenes and the extent of their catabolism and reutilization may factor in the amount of product amassed (8). Volatilized secretions may escape after damage of the cuticle enclosing the droplet or via pores in this structure (6). The diameter and size of glands does not appear to be correlated with exudate accumulation capacity (4).

Ultrastructural features which appear to be common in terpene secreting glands (and also secreting resin duct epithelial cells [4]) are: extended smooth ER; leucoplasts with poorly defined internal membranes, or normal or sometimes unusually shaped but otherwise normal appearing chloroplasts; an association of ER and plastids; and the relative absence of golgi (4). Leucoplast structure appears to vary depending on whether or not monoterpenes are produced (6). We note that the ultrastructure of trichome glands from the mutant, glandular, but nonsecreting tobacco T.I. 1406 is similar to that of secreting types except for the absence of normal chloroplasts (20). Interestingly, transfer of a single gene via plant breeding restores secretion and normal chloroplasts in this mutant (20). Most evidence indicates that synthesis of the terpene precursor isopentenyl pyrophosphate occurs in the cytosol. This intermediate then appears to be utilized by plastids or plastid-ER aggregates to synthesize secreted products (8).

BIOSYNTHETIC PATHWAYS OF GLAND CELLS: WHAT DO WE KNOW?

If we are to hope to manipulate trichome gland cells to modify or extend their metabolic capabilities, we must define and ascertain the limits of their metabolic potential. Looking again to the tobacco and mint systems, we may ask which metabolic pathways other than carbon fixation and isoprenoid synthesis are functional in mature secreting gland cells. Perhaps in developing gland cells undergoing division and proliferation most key metabolic pathways function. But as glands mature and begin to secrete specific compounds, their metabolism may be modified and become more specific. This is suggested from recent findings that short branched and straight chain acyl acids of tobacco-exudate sucrose esters are products of modified branched-chain amino acid metabolism/catabolism (14). In mature gland cells, pathways for synthesis of valine, leucine, and isoleucine appear to be diverted to form CoA-activated acids for esterification in sucrose ester formation. We have suggested that normal flow of carbon to amino acids is diverted somewhat in mature glands due to the lack of a sink for branched-chain amino acid (lack of protein synthesis) or a lack of transaminase to convert ketoacid intermediates to amino acids (14, 15). Keto acids activated by ketoacid dehydrogenase are usually destined for catabolism to recover carbon of branched-chain amino acids as succinyl CoA, acetyl CoA, or acetoacetate. In gland cells this pathway may be blocked to allow use of CoA activated acids for esterification to sucrose (14, 15). Recently, studies of glucose ester synthesis in tomato tissue bearing trichomes support the role of branched-chain amino acid metabolism in C_4 and C_5 acyl acid formation (26). In tomato, straight and branched chain C_{10}, C_{11}, and C_{12} acids are also formed and esterified in glucose esters. These are suggested to be derived from fatty acid metabolism by addition of C_2 units to branched-chain, amino-acid-pathway-derived primers. Kaneda (16) had shown earlier that short, branched-chain acids can serve as primers for $>C_{27}$ hydrocarbon synthesis in tobacco (also *Bacillus subtilis* and *Micrococcus lysodeikticus*) and concluded that elongation involved either addition of C_2 units to primer acids or condensation of these with C_{16} or C_{18} straight chain acids derived from fatty acid synthesis. Thus, mature gland cells of at least tomato may contain active fatty acid metabolism. However, at this time it is not clear if this metabolism is modified to produce C_{10} to C_{12} acids instead of the usual $\geq C_{16}$ products or if normal fatty acid metabolism contributes normal long chain acids via condensation reactions and the products are subsequently shortened via β-oxidation after CoA activation. While it has not been directly demonstrated that acyl acids or glucose esters of tomato exudate are produced in trichome gland cells, results obtained with the tobacco system (14, 15) suggest that this is probably the case.

Thus, evidence exists for pathways of carbon fixation, isoprenoid, branched-chain amino acid, and fatty acid metabolism in secreting gland cells. Mitochondrial function to produce ATP and NADH is needed based on the energy demands of isoprenoid metabolism alone. Gland cells of tobacco and other high-level accumulators appear to have a normal complement of mitochondria (4, 20). Clearly, further study is needed to define the metabolic capability of secreting gland cells but one can already begin to consider modification of isoprenoid metabolism, reactions which modify terpene skeletons, and branched-chain amino acid metabolism (in sugar ester producers) to alter exudate chemistry.

Recent studies from Croteau's laboratory on localization of enzymes involved in monoterpene biosynthesis have used gland isolation and histochemical techniques to show that (−)-limonene cyclase and (−)-limonene hydroxylase, key enzymes in the synthesis of (−)-carvone in spearmint, are local-

ized exclusively in gland cells (8). A number of other monoterpene biosynthetic enzymes have been shown to be enriched in isolated gland preparations including several highly substrate-specific terpene cyclases (7).

The best evidence for metabolic turnover of glandular secretions comes from the work of Croteau and colleagues using the mint system (2). Two types of monoterpene turnover have been distinguished. In immature tissue diurnal fluctuation thought to be synchronized with photosynthesis is observed, but synthesis exceeds loss resulting in accumulation. Late in development a net decrease in monoterpenes is observed. In *Mentha piperita* a major secreted component, l-menthone, is converted to l-menthol and the water soluble neomenthol-glucoside which is transported out of the gland. The extent of higher terpene turnover in glands which produce these compounds has not been studied.

Low incorporation of radiolabeled carbon donors has long plagued attempts to study metabolism of trichome exudate components. This has been attributed to poor access of exogenously supplied precursors to glands and compartmentation within the gland itself (see Croteau and Johnson, 22). Slow turnover numbers for enzymes of the terpenoid pathway might also be a factor. It is also possible that new synthesis is inhibited by existing accumulated exudate. In this regard, an interesting observation was made in recent studies of glucose ester metabolism in tomato. Young leaves were briefly washed with 100% ethanol prior to labeling to remove all but 10 to 20% of exudate (26). While comparison of incorporation of donors in washed *versus* unwashed leaves was not reported, washing presumably did not inhibit biosynthetic capacity of gland cells. Levels of incorporation of ^{14}C-valine were not reported but incorporation of stable isotopes used was said to be substantially improved by the washing procedure. Perhaps partial removal of preexisting exudate can increase incorporation in tracer experiments in other systems and thereby facilitate further characterization of gland metabolism.

TRICHOME EXUDATE AND PLANT-INSECT, -MICROBE INTERACTIONS

My purpose here is not to attempt to survey the vast literature on plant-insect, plant-microbe interactions related to trichome secretions. I only attempt to provide a very brief description of "one plant physiologist's view" of this very important aspect of trichome biology. (Some detailed reviews on the subject are found in references 3, 22, 25 and references therein.)

Interactions between terpenoids and insects are complex. Growth and development of many insects is regulated by terpene-containing substances and terpenoids can attract, repel, cause alarm, or initiate defense reactions in different insects (see Kelsey *et al*, 22). Many insects are dependent on plants as a source of sterols since they are incapable of synthesizing the sterol nucleus (4). While the effects of exposure to terpene compounds on insects can range from attractant to toxin, specific responses can depend on insect species, concentration, other chemicals present, and on the mode of contact. Extensive studies have been made in a number of systems to evaluate the influence of specific exudate chemicals on specific insects. These have involved comparisons of insect behavior and exudate composition in natural and experimental populations of plants, studies comparing insect response with intact tissue *versus* tissue with exudate removed or tissue with exudate removed and specific purified components added back. Injection, topical application, or inclusion of exudate components in artificial diets have been used as approaches to study effects of exudate components on reared insects. Despite complexities involved in studying systems containing more than one organism, many tissues, etc., clear effects of exudate components have been established from studies of potato (25), tobacco (3), tomato (9), and several other species. For example, Goffreda *et al.* (9) recently compared potato aphid behavior on the wild tomato *Lycopersicon pennellii,* domesticated *Lycopersicon esculentum,* and an F_1 hybrid of these. Aphid feeding behavior on *L. pennellii* and the hybrid (possessed type IV, sugar ester-producing trichomes of *L. pennellii*) was characterized by a delay in initiation of feeding and in reduced feeding time. Removal of exudate from *L. pennellii* resulted in increased feeding and its application to *L. esculentum* decreased feeding. In this example, behavior of this insect appears to be primarily dependent on chemistry of exudate of one trichome type. In contrast, insect avoidance/deterence in potato appears to result from different physiochemical and chemical properties of two different types of trichomes (25). Exudate terpenes, essential oils, and sugar esters are often sticky in nature and have long been known to entrap insect pests. For this reason, exudates having both sticky properties and insect-interactive chemicals are said to comprise a physiochemical defense mechanism (25). It is not surprising that insect resistance mechanisms involving trichomes are complex and highly variable.

In a different approach to understanding the basis of insect resistance, Goffreda *et al.* (10) recently used graft chimeras to determine the contribution of various leaf surface tissues to insect resistance. They prepared periclinal chimeras of aphid-susceptible *L. esculentum* and aphid-resistant *L. pennellii* to determine if resistance required interaction of trichome-bearing epidermal with subepidermal tissues or was solely dependent on the presence of epidermal glucose ester secreting trichomes as had been concluded earlier. Though aphids feed by inserting their proboscis into subepidermal tissue, it was found that epidermal features alone accounted for aphid resistance and resistance was correlated with the occurrence of trichome-secreted glucose esters.

The antibiotic and antimicrobial potential of essential oils was recognized early and plant extracts are thought to have been the first preservatives used by man. Mono-, sesqui-, di-, and triterpenes, sesquiterpene lactones, flavones, and isoflavones have been shown to have antibiotic or antimicrobial activity toward certain organisms. It is probable that most of these compounds are products of glands but some may be produced by epidermal cells and then secreted through the cuticle as with surface waxes. In several cases studied, the response of microorganisms to exudate compounds have been compared *in vivo* and on plant tissue as in the case of the sesquiterpene lactone parthenolide from *Chrysanthemum parthenium* (see Kelsey *et al.*, 22). The possibility that trichome exudate components may function as plant growth regulators and alleochemicals has also been discussed (3, and Kelsey *et al.*, 22). Finally, nicotine-related alkaloids are sig-

nificant pest-interactive components of *Nicotiana* and *Petunia* trichome exudates. Alkaloids, phenolics, and lignans are thought to be important insect-interactive components secreted or accumulated by trichomes of certain plants (see Kelsey *et al.*, 22).

FUTURE STUDIES

As we become more familiar with the metabolic potential of trichome gland cells, we may be in a position to transfer from one genus or species to another genes encoding enzymes which can provide modified metabolites having superior pest or pollinator interactive properties. Or, we may be able to introduce novel modifications to endogenous components, thereby producing new compounds. To reiterate, certain plants can amass high levels of trichome exudate. With tobacco, for example, using standard cultural practices and a variety yielding 10% of leaf dry weight as exudate, it is theoretically possible to obtain about 225 kg of exudate per hectare. A number of tobacco varieties possess both high biomass and high exudate accumulation potential. Exudate can simply and cleanly be recovered by submersion of the plant in noninvasive solvent, again, because this material is essentially accumulated outside the plant.

Plant breeding has been used successfully to manipulate trichome numbers and exudate composition in a number of cultivated plant species. Often these efforts have involved attempts to retrieve from wild species trichome related, pest-resistance-conferring traits which were lost as a result of selective breeding. An alternative to this approach is to attempt direct single gene changes using recombinant DNA methods. Such attempts at modification may require the use of trichome-specific promoter elements which will probably be available in the near future. Alternatively, changes which impact only on metabolic steps restricted to exudation (*i.e.* an enzyme specific to exudate compound synthesis) may not require such promoters. To this author, the real challenge to those wishing to cause substantial modification of trichome secretion using the recombinant DNA approach is not in devising or applying molecular techniques. Rather, it is in identifying those simple changes of existing metabolism which may have substantial and desirable impact. Clearly, more study is needed to better define existing metabolism of gland cells to expand the possibilities. Finally, experiments to introduce novel genes into gland cells will undoubtedly provide a greater understanding of processes governing exudate formation and secretion.

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