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Morphological, Pharmaceutical and Protective Mechanism of Trichomes in *Lycopersicon Species*

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Abstract:

Trichomes on plants are epidermal outgrowths of various kinds and use basically to deter herbivore attacks via physical and/or chemical means in addition to producing various chemicals response to the internal and external stresses/stimuli. Study of trichome morphology and pharmacological significance has becoming an important area recently. Towards this end, a large number of tomato lines including cultivars and wild species (>1200 lines) screened for TLCV transmission, under glasshouse and field conditions. TLCV resistance lines showed that resistance is due to the vector deterrence, but not to the virus. Thus, leaf morphology of selected tomato plants, were characterized by both light and scanning electron microscopy. Types of trichomes, structure, pattern of distribution and their potential role against biotic and abiotic factors on tomato leaf surfaces have been characterised. Association of glandular trichomes with physical resistance to vector *Bemisia tabaci* was established. Capitate (glandular) trichome stalk connected with a large spherical head, filled with toxic fluid found to be very effective in insect deterrent. Glandular trichome VIc type mainly present on the *L. hirsutum*, showed physical resistance to whiteflies. In contrast, nonglandular trichomes provide protection against abiotic factors (e.g., lowering of evapotranspiration) and to the biotic factors (e.g., deterrence to insects) of different types. But the glandular trichomes in particular are more interest to investigate further to exploit the potential uses against both biotic and abiotic factors and also for exploitation of secondary metabolites for various other uses.

Keywords **—Glandular trichomes, *Lycopersicon*, TLCV, Whiteflies, deterrence.**

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INTRODUCTION

Plants have the unique ability to synthesize various chemicals (carbohydrates, proteins, fats, etc.) required for most life activities, thus, they are the most resourceful organisms for other life forms. Because of these and other reasons, plants are constantly invaded by all the heterotrophs. In addition, plants have inhabited in diverse geographical regions and have static life, thus, they have evolved various mechanisms to cope up with all the environmental adversities during their lifecycle. Because of these and other reasons, plants posse's very elaborate and sophisticated mechanisms to protect from both biotic and abiotic stresses. Being resourceful organisms, plants are highly vulnerable to various insect pests and pathogens and suffer from frequent environmental stresses. Among many diverse resistance mechanisms evolved to overcome these unwarranted dangers, many morphological structures that provide resistance mechanisms found very effective. One among such mechanisms is the development of trichomes or leaf hairs on plant surface. Trichomes are epidermal hairs found on the aerial surfaces of nearly all plants. These are superficially similar to the hairs on the human body.

Trichomes are unique and dispersed cell types appearing during differentiation of the vegetative and reproductive organs in the epidermal cell layer. A trichome can be defined as any structure that originates as a local outgrowth of the epidermis, most often of a single epidermal cell, including hairs, scales bladders, spines and glands (Mauseth 1998). Trichomes are diverse structures that may be tumescent, globular, unicellular or multicellular, branched or unbranched, glandular or nonglandular. Evidence for trichome function is circumstantial, but they probably serve a range of functions including protection from UV light damage by scattering UV irradiation. The trichomes can act as physical and chemical deterrents for predators and act as physical structures to prevent water loss and protect from the heat. Most importantly, they produce a array of chemical compounds with diverse functions and have potential to commercial exploitation.

Because of their usefulness and amenable for genetic manipulations, study of trichomes have become very important area in modern plant sciences. During this investigation, as a preliminary study, the morphological features of trichome types on different tomato genotypes have been studied using light and scanning electron microscope and their role in insect resistance has been evaluated by screening of different species in the laboratory as well as by field studies.

Developmental Biology of Trichomes

Trichomes are an excellent model system to study development because they are of epidermal origin, and are therefore easily accessible. In addition, trichomes are not essential for the plant under laboratory conditions, which facilitates the isolation of trichome-specific mutants. Trichomes, like stomata, are regularly spaced throughout the leaf epidermis and initiate from the smaller daughter of an asymmetric cell division, termed a trichome precursor cell (Sachs et. al., 1993). The genetic molecular and cell-biological analysis of trichome development has revealed only a few trichome-specific processes, as most developmental steps involve the regulation of general cellular machines. Therefore, studying the trichome system has provided unique insights into the function of transcription factors, the microtubule and actin cytoskeleton, the cell cycle and cell-death control. The study of all the developmental stages of a single cell is a first step towards an understanding of how general cellular processes integrated during development. In Arabidopsis, the trichome precursor cell first undergoes several rounds of DNA replication without intervening mitoses (endoreduplication). As a result, the trichome cell increases in size and changes its direction of growth such that it grows perpendicular to the leaf surface. As the precursor cell expands out from the leaf surface, the enlarged nucleus migrating toward the tip of the expanding trichome (Hulskamp et. al., 1994; Marks 1994). Frequently cells near the base of the trichome, termed accessory cells, differentiate further as part of the trichome unit. Patterning mechanisms are most likely linked to cellular determination (Figure 1). Trichomes have been particularly amenable to genetic methods of analysis, thus, mutations in approximately 24 genes have been shown to alter various aspects of trichome development in Arabidopsis (Marks 1994). Mutant phenotypes indicate that most of these genes function during trichome morphogenesis, well after trichome cell fates have been determined.

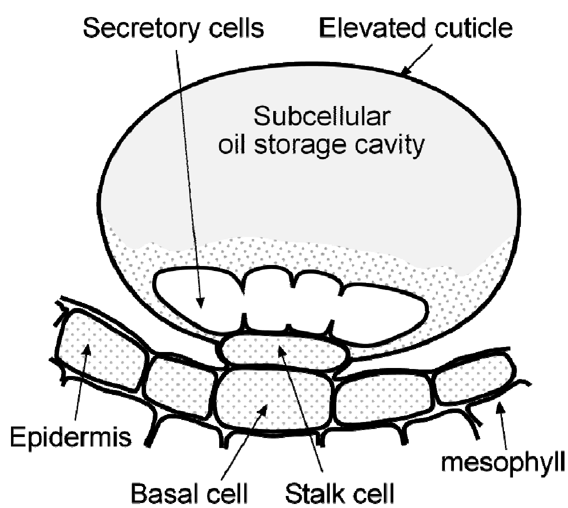

Figure 1 Schematic of a peltate glandular trichome of peppermint.

Glandular Trichomes

Trichomes are unicellular or multicellular appendages, which originate only from epidermal cells, develop outwards on the surface of various plant organs, and can be found on all parts of the plant. Their major distinction is between glandular and non-glandular trichomes. The glandular trichomes in particular are very interesting for various reasons. The secretary product of glandular trichomes often includes highly concentrated secondary metabolites with biological activity of interest to the pesticide, pharmaceutical, and flavour and fragrance industries. Besides these industrial uses, glandular trichomes on some crops confer resistance against insect pests. Thus, recently an increasing interest in understanding the chemistry of glandular trichomes exudates and taking advantage of their potential industrial uses. Bourett et al. (1994) provided an example of the development of the glandular trichome that apparently sequesters a compound that can be readily reduced to the sex pheromone of an economically destructive insect. The study of cell biology, biochemistry and the chemical contents of glandular trichomes, and their role in chemical ecology may lead to a better understanding of natural plant protection and other useful biological activity.

Glandular Trichomes and their Pharmaceutical Industry

Trichomes are epidermal structures that are widespread among plants showing a multitude of functions in physical as well as biological stress responses or ecological interactions (Wagner GJ, 1991). Trichomes are the biochemical factories of the cannabis plant, the most widely used illicit drug worldwide, experiences a renaissance in medical use. For example, tetrahydrocannabinol (THC) is used for the treatment of the symptoms of e.g., neurological diseases, multiple sclerosis or cancer. Other cannabinoids like cannabidiol (CBD), terpenes and phenolic compounds show further pharmacological effects., which make this plant a highly interesting pharmaceutical target. Most of these high-value plant products are synthesized in the disk cells and stored in the secretory cavity in glandular trichomes.

Glandular trichomes in *Mentha piperita* (peppermint), for example, secrete Imenthone, which is converted to I-menthol, and the water-soluble neomenthol-glucoside, which is transported out of the gland. The possibility of manipulating the biosynthesis of Imenthol using recombinant DNA technology may be a boon to industries using menthol, such as cigarettes, liqueurs, perfumes, confectionery, cough drops and nasal inhalers. The protozoan *Plasmodium falciparum*, the human malarial parasite, has evolved resistance to several anti-malarial drugs. Chinese scientists have made good progress in identifying an anti-malarial chemical, artemisinin, from the glandular trichomes of the wormwood, *Artemisia annua*. In a recent study artemisinin was found to cure 143 cases of chloroquinine-resistant falciparum malaria and 141 cases of cerebral malaria. Of 2099 malarial cases tested (*P. vivax* and *P. falciparum* in a ratio of 3:1) all were cured after treatment with artemisinin. Body temperatures returned to normal within 72 hours of treatment and in addition to relieving the symptoms, artemisinin also eliminated the asexual parasite from the blood in less than 5 days after the beginning of the treatment.

Glandular Trichomes and Insect Resistance in Crops

Although the majority of work aimed at understanding trichome function has focused on the specialized metabolites produced within the trichome, more recent studies have demonstrated that proteins involve in defense. Plants may need protection from various external factors, such as herbivores, pathogens, extensive light, and extreme temperatures. Therefore, densely spread nonglandular trichomes may serve as a mechanical barrier against most of the aforementioned factors (Werker 2000). Moreover, glandular and non-glandular trichomes are an important first line of defense against herbivorous insects (Werker 2000 and Glas et al. 2012) and the glandular trichomes may serve as a chemical protection against pathogens.

Glandular trichomes vary in the mechanisms by which they confer resistance, include insecticidal and/or repellent effects, as well as behavior-modifying effects such as feeding or oviposition inhibition. When brinjal or potato cut and exposed to the air, the color of the cut surface changes. Phenols in these cut pieces oxidized by atmospheric oxygen and become black. Glandular trichomes on potato and tomato leave release phenols and phenol oxidizing enzymes, which react to form a sticky substance that hardens to entrap small-bodied insects. Aphids for example, are coated with sticky phenols when they land on these plant surfaces. In the struggle to escape, they disrupt a second type of trichome, which releases polyphenol oxidases (PPO). The PPOs oxidize the phenols into quinone, entrapping the aphids like hardening of cement, resulting in its death. Glandular trichomes in tomato produce large quantities of 2-tridecanone, 2-unidecanone and a viscous mixture of acylsugars, which confer resistance against some tomato-feeding insects. These trichomes also release volatile chemicals. One of these volatile compounds is E-beta farnesene, prevents aphids from landing on the plant. Glandular trichomes in catmint (*Nepeta* sp.) produce nepetalactone, closely related to the aphid sex pheromone, nepetalactol. Nepetalactone can be reduced to the corresponding nepetalactol. Scientist in USA and UK trying to increase the biosynthesis of nepetalactone to use nepetalactols in pheromone traps for monitoring of the aphid population. The resinous material secreted by the glandular trichome of some plants coats the plant surface, particularly on immature tissues, to avoid insect infestation. For example, larvae of cottonweed leaf beetle void feeding on the resin-covered leaves of *Populus deltoides*. Proteinase inhibitor proteins, which interfere with herbivore physiology by inhibiting the digestive proteinases of insects and animals, are known to accumulate in many plant tissues, either constitutively or inducible upon wounding or insect feeding. There are also reports of high expression of metallothionein-like genes in trichomes of *Vicia faba* and Arabidopsis (Guo *et al.*, 2003).

The Glandular Trichomes Research and Applications

The plant glandular trichomes function as either repositories or releasing sites of various phytochemicals. Production of these chemicals in cell or tissue culture systems has stimulated many researchers to investigate further in this area. However, this approach has not been too successful due to the lack of information on the genes that control the synthesis of these chemicals. On the other hand, scientists have been successful in transferring glandular trichome-based insect tolerance to tomato (Channarayappa, et al. 1992) and potato cultivars using conventional breeding techniques. Unfortunately, conventional breeding may not always transfer the desired characters alone from the parents to the offspring. Now it has been estimated that about 1-3 genes may be controlling the expression of plant trichomes. Understanding these genes sufficiently to manipulate and transfer them to desirable plants could lead to significant progress in obtaining crops with desired types of trichomes. The knowledge generated during these studies could be used to support biotechnological improvements.

Screening of Tomato Germplasm for Virus Resistance Genotypes

Most conventional and but very effective method of finding genotypes for economic traits is screening the germplasm. Since the resistance genotypes for TLCV found exhausted in all the locally available cultivating varieties, the germplasm collection for screening extended to include large number of breeding lines and *Lycopersicon* wild species collected worldwide. More than 1500 cultivating varieties and wild species of tomato plants collected from various sources in India and from other countries, used as germplasm material for TLCV resistance source. These plant materials were screened for presence of TLCV disease resistance genes throughout the year, but very specifically during the summer seasons, since the TLCV disease severity is very high in summer, due to whitefly population is high, a major vector for TLCV spread. The preliminary field screening was carried out at Main Research station, University of Agricultural Sciences, Bangalore. Those lines, which did not show disease symptoms under field conditions selected and rose under greenhouse conditions. Three–week old seedlings of each selected line by the field tests were further tested for disease resistance by challenging with viruliferous-whiteflies and by graft-transmission with TLCV infected scions. The genotypes of susceptible, field resistance, and field resistance but graft transmission susceptible plants studied further for understanding the mechanism of virus transmission under glasshouse conditions (Channarayappa et al., 1992a). The field and lab testes elucidated that all the lines took infection by grafting with infected scions, though some were displaying resistance to TLCV in the field condition.

Morphological Observations of Tomato Leaf Surfaces for Resistance Factors

To find out the probable mechanisms for some plants showing field resistance but susceptible to graft inoculation, since they are not genetically resistance to virus, leaf morphological studies were made to determine for possible vector resistance characters. The leaf morphology of nine *Lycopersicon* species and eight of their accessions were examined using light and scanning electron microscopy (Channarayappa et al., 1992b). In brief fresh leaflets sampled from equivalent positions of the upper, middle, and lower leaves of each plant. With each pair one leaflet was used to obtain an adaxial trichome count and the opposite leaflet was used for an abaxial surface trichome count. Leaf discs of 4 mm in diameter were cut from freshly harvested leaves with a cork borer. For scanning electron microscope studies, fresh discs were mounted on a stub with vacuum grease. Micrographs of the surfaces of leaf were taken an International Scientific Instruments Super-mini-SEM, at magnification of 100 X. The micrographs were taken within 5 min of reaching an operational vacuum, which avoided processing of fresh specimens from complex processing steps for SEM. The density of trichomes within the interval area near the centre of each leaflet was determined with the use of a dissection microscope at 40 X. Different types of trichomes present on each surface of leaf recorded separately for each plant.

Trichome Types and their Distribution on Leaf Surfaces of Tomato Cultivars and Wild Species

The glandular and nonglandular trichomes distributed all over the vegetative and reproductive organs of tomato plants. However, the density and types varied with location and with developmental stages of a plant (Figure 2). In general, younger leaves have higher densities of trichomes, when compared to older leaves. They type of trichomes on leaves found significantly different in different genotypes. Between two major types of trichomes, glandular and non-glandular, glandular trichomes found effectively immobilizing the whitefly vectors.

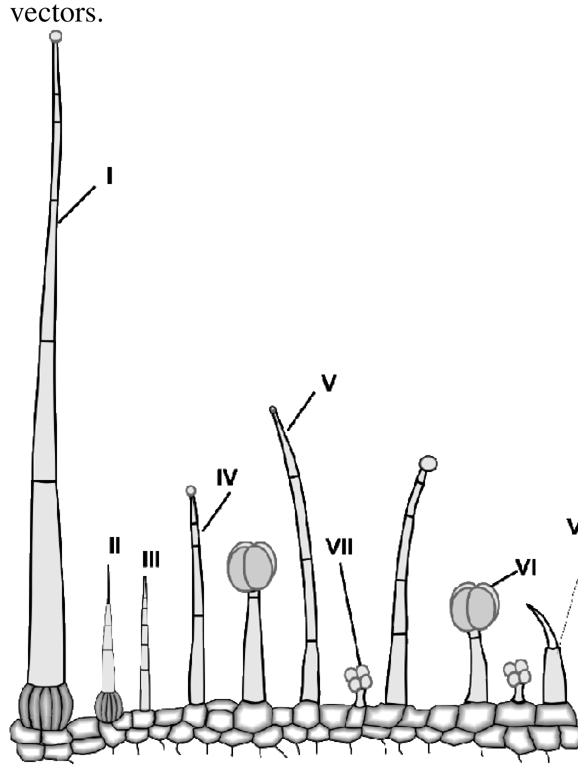

Figure 2 Different types of trichomes present on tomato leaves.

Glandular Trichomes Present on Tomato Leaf Surfaces

Glandular trichomes producing essential oils of commercial value wide spread on leaves and flowers of many terrestrial plants. The glandular trichomes are of two main types, capitate and peltate, which can be distinguished by head size and stalk length. As a rule, in a capitate trichome, the length of the stalk should be more than half the height of the head, whereas peltate trichomes are short with a uni- or bi-cellular stalk and a large secretary head with 4-18 cells arranged in one or two concentric circles (Abu-Asab and Cantino, 1987). Capitate trichomes are very variable in stalk length, head shape, and secretion process, and they further subdivided into various types (Werker et al. 1985). Because of histochemical tests, it has been assumed that capitate trichomes secrete varying amounts of polysaccharides (Werker 1993), in addition to essential oils. Glandular trichomes present on the tomato wild species mostly are of capitate types (Figure 3). Capitate trichomes are composed of one to three stalk cells and one to four-celled glandular head. On maturity, the number of basal cells and the morphology of the stalks quite variable, and these trichomes further divided into two types based on structure and size. Capitate type I trichomes consist of one basal cell, a short stalk cell and a bicellular head. Capitate Type II trichomes possess one basal cell, one to four stalk cells, a narrow neck cell and a globose unicellular head. The lower stalk cell, conical in appearance, is long, exhibiting a smooth surface or cuticular warts. A cellular pedestal formed by 8-32 epidermal cells arranged around the bases support these trichomes. The secretary head attached to the neck, composed of one to two cells and has a narrow diameter. Variability in both the occurrence and the density of type II capitate hairs was observed and the secretary material accumulated in the cell lumen has many biological functions. The secretary product appeared to exude through the head cell cuticle only in type II capitate hairs (Figure 2).

The capitate trichomes, as other trichomes, originate from a single protodermal cell, larger than the neighboring ones. Through a series of periclinal divisions, uninserted row of three to five cells formed. The lower cell of this row corresponds to the trichome basal cell, the upper to the trichome head initial and the intermediates to the stalk. Afterward, the trichome head initial enlarges to form a globose cell and finally it undergoes two successive anticlinal divisions, the second at right angles to the first, to create a four-celled glandular head. On maturity, the capitate trichomes were of two types differing in structure and size. At maturity, the capitate trichome type I are about 40 mM (±20). The horizontal diameters of the head of both trichomes are about 30x40 µM (±10). The secretion accumulates in a small subcuticular space.

Peltate trichomes in other hand consists of a short stalk cell with cutinized lateral walls and a large head with eight secretary cells arranged in a circle (Figure 3). As all trichomes, they originate from a single protodermal cell that suffers a periclinal division. The upper daughter cell of this two-celled primordium divides asymmetrically to give rise to the stalk cell and the trichome head initial. This cell, after a period of enlargement, undergoes successive anticlinal divisions until the head is fully formed. A mature trichome is about 60µM (±5) in height and 50 µM (±10) in diameter at the head. The material produced by the head cells passes through the apical walls and accumulates within a space formed by the apical walls and accumulates within a space formed by the development of the cuticle together with a pectinic layer of the cell wall. The secretory material remains trapped between this relatively thick cuticular sheath and the head cells, giving to each peltate trichome a spherical shape. Cuticular rupture is often observed in SEM micrographs, following a horizontal line of apparent fragility in the diametrical region of the head.

Non-glandular Trichomes

The non-glandular trichomes are uniseriate, multicellular (two to five cells) pointed-shaped, with an average length of 300 µM (±50). A cellular pedestal, formed by a group of 8-32 epidermal cells arranged around the base, supports these trichomes. Although erect, the more distal cells are leaning towards the tips of the leaves (Figure 3). Then cell walls present well-developed cuticular warts. These trichomes are elongated (1100µM ±100), orange-coloured have a variety of functions. The trichome layer may constitute a mechanical barrier against biotic attack, an additional resistance to the diffusion of water vapor from the leaf interior to the atmosphere, or a reflector reducing the radiant energy absorbed by the leaf. In the two latter cases, hairs may have a decisive role in leaf energy balance and water retention, providing the plants with specific ecophysiological advantages, especially in arid and (or) high irradiance environments (Ehleringer 1984). Recently it was shown that leaf hairs from a variety of species contain UV-B absorbing compounds, indicating that besides other functions, the nonglandular trichomes also protect underlying tissues against UV-B radiation damage. It suggested that the dense trichomes often covering young leaves may, in addition to other functions, protect transiently the underlying cells against UV-B radiation damage during the time period required for the maturation of internal avoidance and (or) repairing mechanisms.

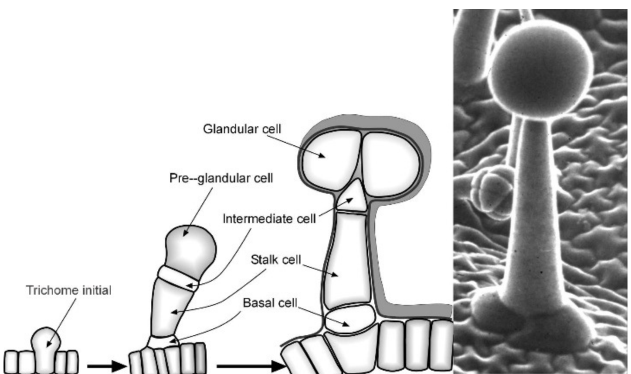

Figure 3 Initiation and developmental stages of tomato Type 6 glandular trichomes from Solanum lycopersicum.

Distribution of the Trichomes on Leaf Surfaces

Glandular trichomes are present on both leaf sides, being predominant on the abaxial surface (lower surface of leaf); where they are particularly concentrated at inter vein areas. (Figure 4). On the veins and leaf margins, glandular trichomes are scarce, while the nonglandular trichomes are abundant. On the adaxial leaf surface (upper surface of leaf), the glandular trichomes are densely distributed and the nonglandular ones are scattered among them. The capitate trichomes of type I are abundant, while those of type II are rare.

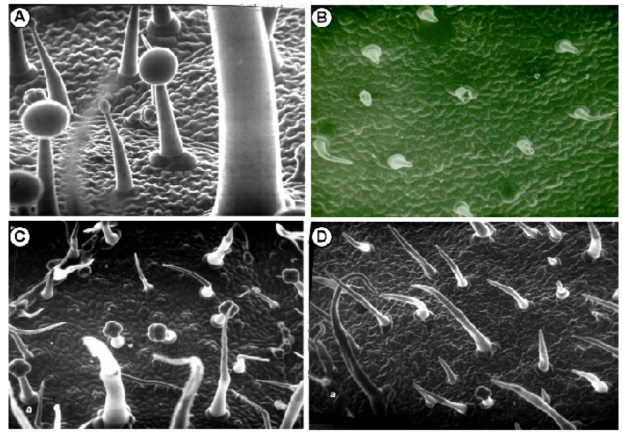

Figure 4 Scamming electron microscopic (SEM) images of tomato leaf trichomes (Channarayappa et al 1986). Trichomes on leaf surfaces of (A) *L. hirsutum*, (B) *L. esculentum*, (C) *L. parviflorum* and (D) *L. chilensis*. **SEM images:** Fresh *L. hirsutum*leaves were directly mounted on specimen holders and scanning electron microscope (SEM) images were immediately recorded on a Quanta 200 F (FEI, OR, USA) under low vacuum mode (130 Pa).

The development of the glandular trichomes forms epidermal initials up to the fully mature phase proceeds fast during the early stages of leaf growth. On very young leaves, numerous glandular trichomes at various stages of development nearly covered by nonglandular hairs that form a dense mat. Observations on SEM micrographs showed that the number of glandular trichomes per leaf-surface unit area (mm^2) progressively decreases with leaf enlargement. On fully expanded leaves, early ontogenetic states of trichomes not observed. Upon maturation of the leaf, peltate trichomes become sunken in the epidermis.

Turning trichomes into factories

Many of the characteristics associated with glandular trichomes have generated interest in using them to engineer the production of large amounts of specialized chemicals or proteins. One appealing feature of trichomes is that they are dispensable structures; trichome-deficient mutants of Arabidopsis and other plants grow normally under controlled environment conditions, which suggests that modifying the original chemistry of the trichomes and engineering them to make and accumulate novel small molecules or proteins will not have deleterious effects on the plant, even if the engineered product would have phytotoxic effects if accumulated in other cell types. In addition, trichomes can be programmed to produce large amounts of specific small molecules or proteins. Coordinated regulation of genes in trichome biosynthetic pathways suggest that successful engineering of metabolism will require the use of appropriate promoters to drive the expression of pathway-modifying enzymes (Gang *et al.*, 2001). Unlike other structures that are specialized for high-level production of specialized metabolites (for example, laticifers and resin ducts), trichomes are accessible to purification and analysis. In addition, there is an increasing understanding of the genetic and physiological regulatory networks that specify trichome differentiation and patterning (Serna and Martin, 2006). Taken together, trichomes offer a unique opportunity to understand and engineer the development of structures that produce and sequester specialized metabolites, and the pathways leading to them. However, unleashing the bioengineering potential of trichomes will require a deeper understanding of the biosynthetic pathways operating in these fascinating chemical factories.

DISCUSSION

As in most of the terrestrial plants, the surfaces of *Lycopersicon* species, leaves carry both glandular and nonglandular trichomes. The selection pressures that caused the evolution of secondary biochemical pathways to produce potent chemical defences also apparently resulted in the evolution of glandular trichomes in some plant species. The general cytotoxicity of many of the compounds present in glandular trichomes necessitated the concomitant evolution of mechanisms of secretion and sequestration to avoid autotoxicity and to deliver the compounds to the proper place. One can speculate that glandular trichomes are largely the result of this evolutionary interaction between chemistry and structure, in response to biotic selection pressures. The functions of glandular trichomes and the compounds that they produce are not always clear. Unlike other trichome types, the relatively sparse coverage of mature plant surfaces by glandular trichomes precludes a direct function as a physical impedance to insects or a means of reducing solar heating or evaporative loss. However, some glandular trichomes produce sticky materials that entrap insects, and others can secrete sufficient resinous material to coat the plant surface, particularly in immature tissue, thus indirectly performing these functions (Neal et al. 1990; Channarayappa et al. 1992). Secretion of phytotoxins by glandular trichomes could be of secondary benefit to some of the producing plants. For example, one of the first compounds demonstrated to play a role in plant-plant allelopathy was 1,8-cineole, a highly phytotoxic monoterpene in the glandular trichomes of salvia species (Muller and Muller 1964) that inhibit their competitors. Developing and very young leaves are particularly vulnerable to attack by insects and pathogens. Glandular trichomes develop exceedingly rapidly on leaf primordia (Duke and Paul 1993, Bourett et al. 1994). As they mature and become more sparsely distributed over the expanding leaf surface. Many of the compounds produced by these structures have biological activity that deters damage to the plant by insects and/or plant pathogens (Kelsey et al. 1984). Those compounds protecting against insects have varied types of biological activities, including insecticidal, repellent, behaviour-modifying and feeding deterrents. Some of the compounds may play roles in plant-insect interactions other than protection, such as attraction of pollinators or other beneficial insects. Many of the compounds produced by glandular trichomes, particularly the terpenoids, are antimicrobial (Kelsey et al. 1984). Essential oils containing these compounds have been used as preservatives and disinfectants. However, constitutive defences against pathogens have not received as much study as inducible defences.

Plant species that produce glandular trichomes generally produce relatively large amounts of bioactive secondary products. The glandular trichomes are the primary production sites of many of these compounds. The secondary products of several biochemical pathways can be found in glandular trichomes of higher plants, although terpenoids seem to predominate. Phenolic compounds from the shikimate pathway are quite common constituents of secretory glands. In some

Solanum species, phenolic compounds released by breakage of specialized glands by insects, resulting in rapid oxidation of the phenolics to quinones by polyphenol oxidase released from gland cell plastids (Kowalski et al. 1990). The phenolic quinones polymerize rapidly enough to "glue" insects to the leaf surface or make their mouth parts-unusable (Channarayappa et al. 1992). Other secondary compounds of glandular trichomes, such as sugar esters of fatty acids play a role in combating plant pests (Neal et al. 1990)

The great diversity of plant trichomes has interested botanists by their adaptive and taxonomic value. In the family *Lycopersicon*, the morphology, distribution and frequency of glandular trichomes used as discriminative characters at sub-familiar level (Channarayappa et al., 1992). Although only a few species have been examined in detail, two main types of glandular trichomes (peltate and capitate) are often described. Peltate trichomes with short stalks and large flattened heads of 4-18 cells, arranged in a disc or in two concentric circles, have been widely reported. These trichomes are in the literature under a variety of names including glandular scales and subsessile glandular trichomes. Despite their common occurrence, peltate trichomes are absent in many species of *Lycopersicon* (Channarayappa et al., 1992). Capitate trichomes are widespread in *Lycopersicon*, but they are more variable in stalk length and head shapes. They generally consist of one to two stalk cells and one to two cells forming a rounded to pear-shaped secretory head.

Peltate and capitate trichomes also have different secretion processes. In the peltate trichomes, the secretory product seems to remain trapped in a large subcuticular cavity, unless external factors such as high temperatures, low air humidity or animal aggression cause the cuticular rupture. SEM studies revealed a straight line at the region of the horizontal diameter of the head, indicating a decrease in the resistance of the cuticular sheath, promoting the release of the essential oil. Capitate trichomes form small subcuticular spaces and the release of the secretory product probably occurs through cuticular microspores. The ontogeny of *Lycopersicon* glandular trichomes follows the pattern described for other species. Trichome production ceases during leaf enlargement therefore the final number of trichomes is established at an early stage of leaf development. Corresponding results have been reported for other crops. The presence of glandular trichomes, particularly by capitate trichomes on *L. esculentum* may act as deterrent for herbivores.

CONCLUSIONS

Most plants have hairs on their aerial surface, called trichomes, on their surface that serve a number of functions ranging from protection against insect pests to heat and moisture conservation. There are two main types of trichomes: glandular and nonglandular. Glandular trichomes contain or secrete a mixture of chemicals, which found to have an enormous array of uses in the pesticide, pharmaceutical, and flavour/fragrance industries. Besides these industrial uses, glandular trichomes on some crop species confer resistance against insect pests. Thus, there is today an increasing interest in understanding the chemistry of glandular trichome exudates and taking advantage of their potential uses. Understanding the way glandular trichomes develop and finally turn into highly efficient biochemical factories in the epidermis of various plant species is of key importance and could lead to more applied outcomes. Increased knowledge of these fundamental aspects will allow researchers to tap the up-to-now largely unexploited biotechnological potential of glandular trichomes to engineer plants that would exhibit increased resistance to pests or that would produce compounds of immense industrial/pharmaceutical interest (molecular pharming).

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