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Plant Glandular Trichomes: The Natural Pesticide Factories

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Abstract

Indiscriminate use of synthetic pesticides has many bad implications on environment and human health. It also leads to development of pest resistance, so glandular trichomes can be used as an important first line of defense against herbivorous insects and pathogens. Glandular trichomes have the capacity to produce, store and secrete large amounts of different classes of secondary metabolites like terpenes, phenylpropenes, flavonoids, methyl ketones, acyl sugars and defensive proteins which are having the potency to act as natural pesticides. It is evident that via breeding or genetic engineering by using, trichome-specific promoters will develop a stronger grip on how to obtain the desired levels of biocides in a tissue-specific manner.

Introduction

Virtually all plant species possess some kind of hair-like epidermal structures. When these structures are present on the aerial parts of a plant, they are commonly referred to as trichome. Trichomes vary in size from a few microns to several centimeters and exhibit a tremendous species-specific diversity in shape. Trichomes are mainly found on leaves and stems, but they can also occur depending on the species on petals, petioles, peduncles and seeds. Trichomes can be single-celled or multi-cellular, but the criterion that is mostly used to classify them is whether they are glandular or not. Non-glandular trichomes are present on most angiosperms which are unicellular and can be either unbranched or have two to five branches. In contrast, glandular trichomes are usually multicellular, consisting of differentiated basal, stalk and apical cells and can be found on approximately 30 percent of all vascular plants. Glandular trichomes have in common the capacity to produce, store and secrete large amounts of different classes of secondary metabolites like terpenes, phenylpropenes, flavonoids, methyl ketones, acyl sugars and defensive proteins which are having the potency to act as natural pesticides.

Morphology of Different Plant Glandular Trichomes

Glandular trichomes can be subdivided into capitate and peltate trichomes. Both types are frequently present in the asteraceae, lamiaceae and Solanaceae plants. Capitate trichomes typically consist of one basal cell, one to several stalk cells, and one or a few secretory cells at the tip of the stalk. They predominantly produce non-volatile or less volatile compounds that are directly exuded onto the surface of the trichome. Peltate trichomes, of which typical examples can be found in mint and basil, consist of a basal cell, one (short) stalk cell, and a head consisting of several secretory cells, which is surmounted by a large sub-cuticular storage cavity. This cavity is formed by separation of the cuticle from the cell wall of the secretory cells and it is filled with the products of the secretory cells, thereby giving these trichomes a characteristic "bulb-like" shape.

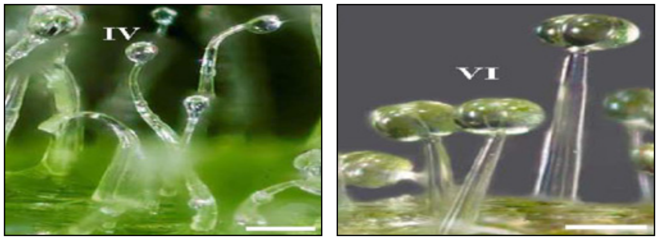

Figure 1: Type IV and Type VI glandular trichome types present on tomato leave surface

Cell walls of stalk cells are usually cutinized, presumably to prevent contact of trichome-produced compounds, which can be auto toxic, with other parts of the plant. The trichomes of the Solanaceae have been studied in detail, especially those of Solanum species, because of their role in plant resistance. Typically, eight different types are distinguished of which four (i.e., type I, IV, VI and VII) are glandular capitate trichomes and four (i.e., type II, III, V and VIII) are non-glandular. The glandular trichome types differ in number of stalk and secretory cells (see Table 1 for a description of trichome morphology), as well as in their chemical contents (Glass *et al.*, 2012).

Table 1: Description of different type of glandular and non-glandular trichomes

Trichome Type	Description
I	The glandular trichomes consisting of 6-10 cells and 2-3 mm long. Globular and multicellular base with a small and round glandular cell in the trichome tip.
II	Similar to trichome I but non-glandular and shorter (0.2-1.0 mm). Globular and multicellular base.
III	Thin non-glandular trichome consisting of 4-8 cells and 0.4-1.0 mm long with a unicellular and flat base. External walls lack intercellular sections.
IV	Similar to trichome I but shorter (0.2-0.4 mm) and with a glandular cell in the tip. Trichome base is unicellular and flat.
V	Very similar to type IV with respect to height and thickness but non-glandular.
VI	Thick and short glandular trichomes composed of two stalk cells and a head made up of 4 secretory cells.
VII	Very small glandular trichomes (0.05 mm) with a head consisting of 4-8 cells.
VIII	Non-glandular trichome composed of one basal and thick cell with a leaning cell in the tip.

Biosynthesis and Function of Glandular Trichome-Produced Compounds

The plant epidermal surface represents the first barrier for pathogens and arthropod herbivores to overcome after arrival on a plant. Therefore, it may not come as a surprise that trichome density is one of the main factors correlating with resistance to herbivory. The presence of trichomes is, however, not always beneficial for the plant, since trichomes may interfere with indirect defense by disturbing natural enemies of herbivores. Trichomes can contribute to plant defense in different ways. Non-glandular trichomes can physically obstruct the movements of herbivorous arthropods over the plant surface or prevent herbivores to reach the surface with their mouthparts. Moreover, arthropods may become entrapped in sticky or toxic exudates, such as acyl sugars or polyphenols, produced by glandular trichomes. Such polyphenols are quickly formed via oxidation when the contents from the glandular trichome heads are released as a result of insect-mediated rupturing of the glandular cuticle. The entrapped herbivores usually die as a result of starvation or of ingested toxins or in the case of small herbivores, of suffocation. Alternatively, in some cases trichome-produced toxic compounds were found to be transported via the stalk to distal plant tissues, thereby increasing resistance of these tissues against plant attackers, as shown for pyrethrins in the plant pyrethrum (*Tanacetum cinerariifolium*). It appeared that such pyrethrins, produced by glandular trichomes on pyrethrum fruits, can be taken up by the seed and be transmitted to the seedlings, which lack glandular trichomes themselves, resulting in inhibition of fungal growth and of feeding by herbivorous arthropods. Glandular trichomes, thus, function as important chemical barriers for plant parasites. The main classes of secondary chemicals that have been found to be produced in trichomes include terpenoids, phenylpropenes and flavonoids, methyl ketones, acyl sugars and defensive proteins. Although all of these compounds play a role in plant defense, both glandular and non-glandular trichomes may have many other functions as well, including attraction of pollinators, protection against UV due the presence of flavonoids and other UV-absorbing compounds in trichomes, temperature regulation and reduction of water loss. Furthermore, the ability of some plants to tolerate high levels of metals is correlated with their ability to sequester these compounds in their trichomes, as shown for the rough hawk bit (*Leontodon hispidus*), which can sequester calcium, and tobacco (*Nicotiana tabacum*) which is able to secrete cadmium and zinc via its trichomes.

Terpenes

The majority of terpenoids are secondary metabolites and have functions related to plant defense. Wild potato (*Solanum berthaulti*) repels *Myzus persicae* from its surface due to secretion of some glandular substance i.e. β-frenescence which is a terpenoid compound (Gibson and Pickett, 1983).

Phenylpropenes

Phenylpropenes are well known for their role in the attraction of pollinators. For example, Methyleugenol from the orchid *Bulbophyllum cheiri* was shown to attract several fruit fly species (*Bactrocera spp.)* for pollination. Eugenol which a polyphenolic compound secreted from *Ocimum suave* act as a repellent against stored grain beetles like, *Sitophilus granarius*, *Sitophilus zeamais* and *Tribolium castaneum*.

Flavonoids

Accumulation of flavonoids in trichomes may serve to protect plants from UV-Band there is evidence for sunlight-induced secretion of flavonoid glycosides by glandular trichomes of *Phillyrea latifolia* plants to protect them against damage induced by UV-A. Also, these compounds inhibit the growth of lepidopteran larvae.

Methyl Ketones

Methyl ketones constitute a class of fatty-acid derived volatile compounds that are very effective in protecting plants against pests. The secondary metabolite 2-tridecanone which is a methyl ketone compound was lethal to several herbivorous arthropods, including the tobacco hornworm (*Manduca sexta)* and the cotton aphid (*Aphis gossypii*). Two-spotted spider mite get poisoned when comes in contact with methyl ketone secrated from glandular trichomes of plant. Trichome exudates and 2-tridecanone applied on artificial membranes inhibited feeding and caused mortality of the potato aphid (*Macrosiphum euphorbiae*).

Acyl Sugars

Sugar esters, also called acyl sugars, are nonvolatile metabolites, produced and stored in glandular trichomes of many Solanaceae, including Solanum, Nicotiana, Datura and Petunia species. Acyl sugars may be directly toxic to herbivores, but they are also excellent emulsifiers and surfactants and may easily stick to arthropod cuticles thereby immobilizing or suffocating arthropods. Also, it was shown that acyl sugars can deter or repel herbivores, such as the potato aphid. Structure and activity studies revealed that acyl glucoses and acyl sucrose's were equally repellent to the aphid and differences in the length of the fatty acid chain did not influence repellency (Weinhold and Baldwin, 2011).

Defensive Proteins

Apart from secondary metabolites, trichomes are also able to produce significant amounts of proteins with defensive functions, such as proteinase inhibitors (PIs), polyphenol oxidases (PPOs) and phylloplanins. PIs can be either constitutively expressed (e.g., in flowers) or induced upon wounding or herbivory in leaves and their trichomes and induced PIs slow down the growth of herbivores upon ingestion probably via inhibition of digestive proteinases in the herbivore gut. PPOs constitute a class of enzymes that utilize molecular oxygen for the oxidation of mono- and O-diphenols to O-dihydroxyquinones. PPOs are stored in leucoplasts whereas their phenolic substrates are present in the vacuoles. When the tissue is damaged, for instance by walking herbivores, the PPOs will mix with vacuolar content of the head cell and rapidly oxidize o-dihydroxyphenolics to the corresponding O-quinones. These quinones, in turn, are highly reactive molecules that covalently bind to nucleophilic $-NH_2$ and -SH groups of molecules such as amino acids and proteins, thereby reducing the availability of essential amino acids to the herbivores and/or the digestibility of proteins, or perhaps interfering directly with enzymes.

Hormonal Regulation of Induced Defenses in Trichomes

In the literature, often two forms of plant defense are discriminated. The first are the constitutive defenses, i.e., those defenses that are always present (such as trichomes), and the second are the induced defenses, which are activated or increased upon attack by herbivores or pathogens (such as some parts of the trichome metabolism). Typically, wounding and/or herbivore infestation activates the octadecanoid pathway, resulting in increasing levels of Jasmonic acid (JA) which triggers the expression of defense genes, such as protease inhibitors (PIs), as well as the accumulation of secondary metabolites, like terpenoids. Besides regulating herbivore-induced defense responses, JA is also linked with trichome formation, since JA biosynthesis and reception mutants in the cultivated tomato were shown to have less glandular trichomes while, in addition, herbivore feeding as well as JA treatment can give rise to increased trichome densities on newly formed leaves.

Conclusion

Glandular trichomes are an important first line of defense against herbivorous insects and pathogens. Tremendous progress in the availability of genomic data has allowed for the discovery of genes in various biosynthetic pathways involved in trichome-produced compounds. However, the full potential of trichomes has not been exploited even remotely since plant secondary metabolism is complex and multi-layered while our knowledge on the precise actions of the different members of large gene families and on the rate-limiting steps in pathways is still too incomplete to make the outcome of such manipulations easily predictable. However, it is evident that via breeding or genetic engineering by using, for example, trichome-specific promoters will develop a stronger grip on how to obtain the desired levels of biocides in a tissue-specific manner. Thus, these minute glandular trichomes may soon prove to be the ideal vehicles for targeted modification of the versatile secondary metabolism of many plant species to customize essential oil production and enhance biocide-based protection of crops.

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