Trichomes: targets for breeding biotic and abiotic stress tolerant plants

Deepa P.[1]* & Sanoj E.[2]

[1.]PG Department of Botany, Korambayil Ahamed Haji Memorial Unity Women's College, Malappuram, Kerala - 676122

[2.]PG & Research Department of Botany, The Zamorin's Guruvayurappan College, Kozhikode, Kerala - 673014

*E-mail: deepapsaj@gmail.com

Abstract

Plants possess trichomes on the epidermal layer of aerial parts which includes both glandular and non-glandular types. These unicellular or multicellular structures play predominant role in plant survival by secreting various secondary metabolites during developmental stages of plants. Among the trichomes, glandular type produces the biologically significant metabolic compounds by the expressions of specific genes located in the trichomes that can be up or down regulated by the influence of biotic or abiotic stresses. The stress correlated gene expression makes the plants tolerant to the stresses, which can be isolated and used to produce transgenic stress tolerant plants through genetic engineering.

Keywords: trichomes, glandular trichomes, abiotic stress, stress tolerant plants, glandular secretions.

INTRODUCTION

Trichomes are tiny outgrowths from the plant epidermis ranging from small hairs to larger structures like thorns; but it is typically used to refer the tiny hairs that can be seen emerging from the surfaces of leaves and other epidermal surfaces of plants. The development and specialization of unicellular or multicellular trichomes are largely regulated by a number of transcription factors which include the R2R3 MYB, basic helix-loop-helix protein and WD40 repeat protein. Some of the other factors also regulate the development and differentiation of trichomes that consisting phytohormones, cytokinins, jasmonic acid and salicylic acid (Wagner *et al.*, 2004).The trichomes vary in size, morphology, origin as well as the ability to secrete; similarly, the shape of the trichomes include straight, peltate, stellate, clavate, falcate, strigose etc. The multicellular trichomes are with three differentiated parts *viz.* head, stalk and base in which the base originates from single multiple cells of epidermis. The stalk may be uni or multi-seriated and terminates on head cell with or without secondary metabolites (Fig. 1). In contrast, the unicellular trichomes initiate from single cell of epidermis by possessing basal and head region (Wang *et al.*, 2021).

Based on the secretory potential, there are two types of trichomes viz. glandular and non-glandular. The unicellular or multi-cellular glandular trichomes are known to secrete

various metabolic compounds including water, nectar, resins, mucilage and terpenes. Unicellular glandular trichomes show morphological differences between apical and basal part of the cells; and sometimes, they occur as branched or unbranched pattern. While, multicellular glandular trichomes appear as outgrowths of the epidermis with a head consisting of cells that secrete and store great amounts of specialized metabolites and possess the multicellular base (Wagner, 1991).

Non-glandular trichomes play different functions in different environments to protect the plants. They also vary in shape, size and length, and can be found in a variety of plants. The trichomes provide shade and trap a layer of air over the leaf surface to retain a humid layer and reduce water loss by evaporation even when stomata remain open. Like the glandular trichomes, non-glandular trichomes also exist as unicellular, multicellular, branched or un-branched. A majority of the non-glandular trichomes have been shown to be branched like a star. As for the un-branched non-glandular trichomes, they can exist as uniseriate, biseriate or multiseriate (Fahn, 1986).

The epidermal structures present on aerial plant parts perform various functions like reduce heat load, enhance water absorption, increase tolerance to freezing, protect plant structure from harmful natural effects andresist plants from herbivorous and pathogens (Kennedy, 2003). However, the glandular trichomes produce secondary compounds that are helpful for pollination, defense and protection (Mahlberg & Kim, 2004). The nature of trichome and its secretory substances vary among species and are used in systematics (Wagner, 1991). Glandular trichomes on leaves are extensively studied in many families like Lamiaceae (Modenesi *et al.*, 1984), Solanaceae (Adedeji *et al.*, 2008), Verbenaceae, Asteraceae and Cucurbitaceae (Kolb & Muller, 2004); whereas on reproductive organs the occurrence of trichomes are limited (Werker & Fahn, 1981); even though, the floral trichomes help to keep flower bud in its proper shape until the emergence of full bloom (Tan *et al.*, 2016).

Trichome morphology in economically important plant families

The plants coming under the families Cucurbitaceae, Solanaceae, Verbenaceae, Lamiaceae, Fabaceae and Asteraceae are with different types of trichomes which make the species more important medicinally and in-turn induce abiotic stress resistance (Table 1). The plants bear both glandular and non-glandular trichomes that makes the plant more survivable in harsh environmental conditions of today together with the production of secondary metabolic compounds (Tian *et al.*, 2017).

Fig. 1: Structure of a multi-seriate glandular trichome with base, central stalk and typical head

Cucurbitaceae: The species of Cucurbitaceae possess trichomes on leaves and stem with varying micromorphology including unicellular to multicellular, conical to elongated, smooth to ridges, with or without flattened disk at base and cystolithic appendages, thin to thick walled and

curved at apices to blunt. The family includes about 800 species under 130 genera and most of them are economically important. The economic value depends to the presence of glandular trichomes in the aerial parts and the production of secondary metabolites (Adebooye *et al.*, 2012). *Benincasa hispida*, *Citrullus lanatus*, *Cucumis melo* var. *agrestis*, *C. sativus*, *Diplocyclos palmatus*, *Edgaria dargeelingensis*, *Gynostemma burmanicum*, *G. pentaphyllum*, *G. pubescens*, *Hemsleya dipterygia*, *Lagenaria siceraria*, *Luffa acutangula*, *L. cylindrica*, *L. echinata*, *Melothria heterophylla*, *M. leucocarpa*, *M. maderspatana*, *Sechium edule*, *Thladiantha cordifolia*, *Trichosanthes cucumerina*, *T. cucumerina* var. *anguina*, *T. dioica*, *T. lepiniana* and *T. tricuspidata* possess differently structured trichomes even though the plants are coming under the same family that make the plants unique in economic value. The diversity of trichomes in Cucurbitaceae can be used in solving the taxonomic problem of narrowly delimited taxa as well as can be used as a character state in infrageneric classification (Ali & Hemaid, 2011). Mainly, the distinctive plants exhibit three types of glandular trichomes *viz.* peltate, capitate and conoidal, and four types of morphologically distinct non-glandular trichomes in the leaves and stem. In flower, the non-glandular hairs develop earlier and their density reduces in later stages except in corolla; whereas glandular hairs are predominant in mature flowers. Their differential distribution indicates the significant role of trichomes in effective pollination rather than the mechanical support (Raseena & Beevy, 2018).

Solanaceae: The family Solanaceae has distributed throughout the world and includes many vegetable species which contain both beneficial and toxic alkaloids. In most of the species, trichomes present on leaf epidermal surfaces, petiole, stem, pedicel, sepal, petal, stoma etc. It provides foliar adaptations in plants to survive under specific environmental conditions. Moreover, the trichomes help to identify the plants at species level due to the structural variations among the species within the same genus (Bar & Shtein, 2019). *Capsicum frutescens*, *Lycopersicon pimpinellifolium*, *Solanum macrocarpon*, *S. nigrum*, *S. torvum*, *Nicotiana tabacum* and *Withania somnifera* possess variety of trichomes on leaf, stem and flower (Fig. 2). *S. torvum* and *S. melongena* show stellate non-glandular trichomes on the adaxial and abaxial leaf epidermal surfaces; similarly, the spine-like non-glandular trichomes present in *L. pimpinellifolium* and absent in *L. lycopersicum* (Kaur *et al.*, 2023). In *Nicotiana,* the unique bicellular to multicellular stalked glandular trichomesare very prominent; in contrast unicellular unbranched hairsdistributed on aerial parts of *Capsicum annum* (Liu *et al.*, 2006; Zhigila *et al.*, 2015).

Asteraceae: The plants of Asteraceae possess 35 different trichomes which included in two major categories namely the vegetative and the floraltypes. Three morphologically distinct types of trichomes are distinct on *Tetradenia riparia* leaf surfaces including glandular capitate, peltate and non-glandular (Adebooye *et al.*, 2012). The glandular and non-glandular trichomes are abundant on both the adaxial and abaxial leaf surfaces. Young leaves are densely covered with trichomes; however, the density of trichomes decreases progressively with leaf maturity that indicates the early development of trichomes during the leaf differentiation and the density decreasewith leaf development and age. In *Helianthus annuus*, the glandular trichomes are abundantly distributed on the surface of most plant organs thatconsisting of 6-11 linearly arranged cells whichare
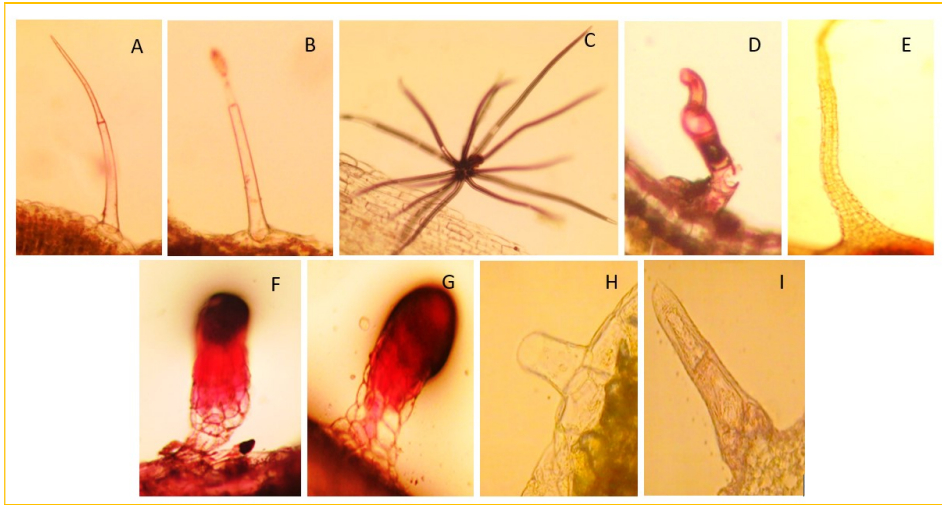
Fig. 2: Structure of trichomes: (A) non-glandular, (B) glandular uniseriate, (C) stellate glandular, (D) horned glandular, (E) multi-seriate non-glandular, (F) dump-bell multi-seriate glandular, (G) multicellular stout glandular, (H) unicellular non-glandular, (I) bi-celled non-glandular trichomes. A, B, C and D are trichomes of Solanaceae species. E, F, G, H and I are trichomes of Lamiaceae species.

associated with the leaf vascular system. Major distributions are along petioles, stems, abaxial surface of chaffy bracts and ray and disc florets in which the highest density shows on the abaxial surface of phyllaries (Amrehn *et al.*, 2014). *Launaea taraxacifolia* never shows any trichome and unique from other species. *Tridax procumbans* exhibits stellate and K-shaped trichomes in abundant (Shafira & Salamah, 2020). The genus *Vernonia* can be delimited from other genera by the possession of T-shaped trichomes, while amoeboid shaped trichomes can be found in the genus *Chromolaena* (Taleb-Contini *et al.*, 2007). However, the trichomeswith cuticular striations on the abaxial surface of *V. amygdalina* and on both surfaces of *Bodenspilosa* are very prominent (Adedeji & Jewoola, 2008).

Lamiaceae: In Lamiaceae members, the correlation between leaf shape and the numbers and size of trichomes are clearly visible. Deeply incised leaves had larger numbers of longer trichomes at the sinuses. Higher numbers of trichomes on upper leaf surfaces occurtogether with trichomes at the petiole and on the abaxial surface. The trichomes of xerophytic species inhibit transpiration in different ways, depending on the number, form, position, whether they are dead hairs or live glandular structures (Mahmoud *et al.*, 2021). The genus, *Salvia* is characterized on one hand by multicellular, uniseriate and scaled dead hairs and on the other hand there are several types of glandular structures, generally with voluminous heads (Janosevic *et al.*, 2016). *Lavandula angustifolia* and *Rosmarinus officinalis* have well-developed ramified forms of dead hairs with different ends and variant levels of flexibility (Zuzarte *et al.*, 2010). The species of *Satureja* are with cone-shaped trichomes, showing predominant glandular trichomes having unicellular base, unicellular stalk and twelve-celled head; while non-glandular trichomes are rare and

few (Bosabalidis, 1990). In *Salvia*, although no glandular trichomes are developed, the plant has numerous simple, uniseriate, multicellular non-glandular hairs (Kahraman *et al.*, 2010). In *Ocimum obovatum*, two types of glandular trichomes present on the leaves viz. large peltate and small capitate. The head of each peltate trichome is made up of four broad head cells in one layer; while the head of each capitate trichome composed with two broad head cells in one layer or a single oval head cell. In peltate heads, secretory materials are gradually transported to the subcuticular space via fracture in the four sutures at the connecting walls of the head cells. In type I capitate trichomes, release of the secretions to the subcuticular space occurs via a pore between the two head cells and release to the head periphery occurs through the opposite pore in the head cuticle. In type II capitate trichomes, the secreted material is released from the head cell through a ruptured particular squared area at the central part of the head cuticle (Naidoo *et al.*, 2013). These secretion modes are reported for the first time in the family Lamiaceae. Histochemically, the secretory materials in the glandular trichomes are mainly essential oils, lipophilic substances and polysaccharides. However, the large peltate trichomes contain a large quantity of these substances than the small capitate trichomes (Kowalski *et al.*, 2019).

Verbenaceae: A species of Verbenaceae, *Lantana camara* is known for its aromatic and medicinal properties. Six morphotypes of glandular trichomes arecommon in the plant that differ in shape, size, number of constituent cells, subcellular aspects and form of accumulation as well as release and composition of the secretion. Idioblasts producing hydrophilic and lipophilic substances in the mesophyll associate with protection of the plant against herbivores and pathogens in turn maintain the water potential of leaf tissues complementing the action of glandular trichomes. The major differences between *L. camara* and *L. radula* are in the distribution of idioblasts. In *L. camara*, secretory idioblasts are distributed in the leaf blades; in contrast, the crystalliferous idioblasts are common in *L. radula* (Passos *et al.*, 2009). In *stachytarpheta cayennensis*, the non-glandular trichomes play significant role in physical protection and participate in the chemical interaction with the environment supplementing the work of the glandular trichomes; while, the peltate and glandular trichomes of *Lippia scaberrima* contain compounds of terpenoid nature are probably the main site of essential oil accumulation. Similarly, five morphotypes of glandular trichomes are identified in *L. origanoides,* and four morphotypes in *L. stachyoides* (Combrinck *et al.*, 2007; Cardoso *et al.*, 2023).

Fabaceae: Simple and gland-tipped trichomes occur in *Medicago lupulina* which are negatively correlated with the amount of damage to leaves in herbarium collections throughout the world, together with the protective role against herbivores (Bar & Shtein, 2019). The species of *Argxrolobium*, *Dichilus* and *Polhillia* are showing differential distribution of trichomes along with varying shape, size and secretions. Trichome type and distribution provide an important insight into taxonomic relations at species level in thegenera. In *Centrolobium tomentosum*, the peltate glands occur on aerial vegetative organs during their primary growth stage which are structurally stable and persisting throughout the development of the organs. During the initial stages of the gland development, cell separation creates a central space that expands as secretions accumulate.

Trichomes without glandular tips are also reported in some species which induces biotic stress tolerance against the herbivores and pathogens (Matos & Paiva, 2012).

Glandular trichomes as source of secondary metabolites

Multicellular glandular trichomes are epidermal outgrowths characterized by the presence of a head made of cells that have the ability to secrete or store large quantities of specialized metabolites. A key and unique feature of glandular trichomes is their ability to synthesize and secrete large amounts, relative to their size, of a limited number of metabolites (Silva *et al.*, 2017). As such, they qualify as true cell factories, making them interesting targets for metabolic engineering.

Gas liquid chromatographic analysis of the oil content of the most numerous gland species indicates only minor quantitative differences in essential oil composition. The major monoterpenes like p-menthanes, pinanes, bornanes and thujanes are characteristic of *Salvia officinalis* (Marchica *et al.*, 2021). Glandular trichomes of *Rubus idaeus* normally produce polyphenols, terpenes, lipids, proteins and carbohydrates; similar to this, *Trichogonia cinerea* secretes volatile oils and phenolic compounds in which the major components identified in the volatile oil are 3,5-muuroladiene (39.56%) and butylated hydroxytoluene (13.07%) (Chwil & Kostryco, 2020). *Tanacetum cinerariifolium* produces a diverse array of pyrethrins and sesquiterpene lactones for plant defense of which the highest concentrations accumulate in the flower achenes that are densely covered by glandular trichomes. The trichomes of mature achenes contain sesquiterpene lactones and other secondary metabolites, but no pyrethrins. During achene maturation, the key pyrethrin biosynthetic pathway enzyme, chrysanthemyl diphosphate synthase is expressed only in glandular trichomes and chrysanthemic acid is translocated from trichomes to pericarp, where it is esterified into pyrethrins that accumulate in intercellular spaces (Ramirez *et al.*, 2013). In *Plectranthus grandidentatus*, three distinct types of glandular trichomes are present on the vegetative organs. Peltate trichomes confined to the leaf abaxial surface, and digitiform and capitate trichomes distribute on both leaf surfaces. In addition to these trichome types, the flowers also exhibit uncommon conoidal glandular trichomes. The secretion shows the presence of terpenoids and flavonoids as main constituents. Essential oils of aerial organs include the sesquiterpenes constituted the dominant fraction (69–79%), β-caryophyllene (9–13%), δ-cadinene (5–7%), β-caryophyllene oxide (4–8%) and 14-hydroxy-9-epi-(*E*)-caryophyllene (4–6%)(Mota *et al.*, 2013). The types, morphology, distribution, structure and development process of the glandular trichomes on the leaves of *Thymus quinquecostatus* are varying distinctly. Two different types of glandular trichomes, capitate trichomes and peltate ones play significant role in metabolite secretions that contained essential oil, polyphenols and flavonoids, while, in addition to these three components, the secretion of the peltate one also contained acid polysaccharides. Moreover, the secretion of capitate one was extruded through the cuticle of the head cell, but the secretion of the peltate one kept accumulating in the subcuticular space of the head cells until it was released by cuticle rupture. The glandular secretions of *Arnica* species are rich with sesquiterpene lactones, phenols and terpenes (Sun *et al.*, 2022). Similarly, *Tussilago farfara* secretes organic acids, sugars, polyols, phenolics, and terpenoids through glandular trichomes by the excessive role of

smooth endoplasmic reticulum and leucoplasts (Muravnik *et al.*, 2016). The glandular secretions of *Sigesbeckia jorullensis* mainly composed of sesqui and diterpenes, with the sesquiterpene hydrocarbon germacrene-ᴅ as the main component that cause stickiness of the essential oil. Permanent glandular trichomes of *Robinia viscosa* var. *hartwigii* produce viscous secretion containing several secondary metabolites as lipids, mucilage, flavonoids, proteins and alkaloids (Muravnik, 2021). Normally, *Lavandula* sp. is an aromatic plant with the chemical composition of monoterpenoids and sesquiterpenoids which are primarily synthesized and stored in epidermal glandular trichomes. These volatile organic compounds are responsible for the aroma characteristics of plant oil that drive consumer preference. Large bulbous peltate and capitate glands of *Lippia scaberrima* containing compounds of terpenoid nature are probably the main site of essential oil accumulation. Moreover, the slender tapered seta with an ornamented surface and uniseriate base are also evidently secretory in nature (Singini *et al.*, 2023).

Glandular trichomes induced abiotic and biotic stress tolerance

Plant glandular trichomes are multicellular secretory structures that arise from protodermal cells and are characterized by a diverse form, localization, density and composition of secreted substances. Formation of the glandular trichomes is caused by the need to protect plants from various biotic and abiotic factors including herbivorous insects, fungi, pathogens, extensive light, UVB radiation or high temperature. The ability of synthesizing and accumulating the various compounds of primary and secondary metabolism makes the plants more tolerant to environmental stresses. To date, more than 100 genes are known to be involved in trichome development including genes that regulate trichome initiation, differentiation, multidimensional cell growth and branching. Most of these genes encode transcription factors that positively or negatively regulate trichome development. Because of key roles of trichomes in plant stress responses, the trichome development-related genes also participate in basic biological responses during the biotic and abiotic stress (Zhang *et al.*, 2021).

The trichome in *Nicotiana tabacum* is a biologically active and stress responsive tissue and play several roles in the defense against biotic and abiotic stresses due to the occurrence of stress tolerant genes of trichomes. Moreover, the glutathione levels in tip cells of both long and short trichomes are always higher than those in other types of leaf cells indicating the presence of an active sulfur-dependent protective system in trichomes. Melatonin is a well-known signaling molecule that mediates a range of physiological activities and various stress reactions in plants. In *Nicotiana tabacum*, melatonin enhances the development of root hairs and glandular trichomes which results in enhanced secretion in glandular trichomes, in turn ameliorate aphid resistance of plants by facilitating the accumulation of cembranoids in the glandular trichomes. In addition to this, melatonin also improves tobacco resistance to high salinity, drought and extreme temperature stresses (Song *et al.*, 2022). Dynamic expression of *NtJAZs* in *N. tabacum* activates by salicylic acid, methyl jasmonate, gibberellic acid and cold, salt and heat stresses. With drought stress, the expression of *NtJAZ-1*, *-2*, *-3*, *-4*, *-5*, *-6*, *-7* and *-8* up-regulates considerably; hence the genes can be focused for genetic engineering to produce abiotic stress tolerant plants (Zhang *et al.*, 2021).

Table 1. Chemical composition of glandular trichome secretions in different plant species

Plant species	Family	Chemical composition
Lippia scaberrima	Verbenaceae	Terpenoids
Cordia verbenacea		Flavanoids
Isodon rubescens	Lamiaceae	Terpenoids, flavonoids, carbohydrates, phenolics and alkaloids
Pogostemon cablin		Lipids, flavones and terpenes
Salvia officinalis		Menthanes, pinanes, bornanes and thujanes
Thymus quinquecostatus		Polyphenols, flavonoids and polysaccharides
Plectranthus grandidentatus		β-caryophyllene, δ-cadinene, β-caryophyllene oxide and 14-hydroxy-9-epi-(*E*)-caryophyllene
Leonotis leonurus		Terpenoids and flavonoid aglycones
Tanacetum cinerariifolium	Asteraceae	Pyrethrins and sesquiterpene lactones
Trichogonia cinerea		3,5-muuroladiene and butylated hydroxytoluene
Sigesbeckia jorullensis		Sesqui and diterpenes
Tussilago farfara		Organic acids, sugars, polyols, phenolics, and terpenoids
Inula helenium		Lipid substances and polyphenols
Helichrysum aureonitens		Flavanoids
Artemisia annua		Sesquiterpene lactones
Helianthus annuus		Germacrolides and heliangolides
Robinia viscosa	Fabaceae	Flavonoids, proteins and alkaloids
Centrolobium tomentosum		Carbohydrate, resin droplets and terpenes
Bauhinia curvula		Phenols and terpenes
Bauhinia rufa		Phenols and terpenes
Trigonella foenum-graecum		Alkaloids, lipids, mucilaginous polysaccharides and phenolic compounds
Erythrina speciosa		Non-reducing sugars
Chamaecrista dentata		Favonoid aglycones
Withania somnifera	Solanaceae	Alkaloids and phenolics
Solanum fernandesii		Polysaccharides, pectins, mucilage, proteins, lipids, resins and phenols
Solanum berthaultii		Sesquiterpenes
Solanum tuberosum		β-Caryophyllene and E-β-Farnesene
Cucurbita pepo	Cucurbitaceae	Lipids, flavones and terpenes
Cucumis sativus		Flavonoids

Both the formation of trichomes and the accumulation of phenolics are interrelated at the molecular level. During the early stages of development, non-glandular trichomes show strong morphological similarities to glandular ones such as the balloon-like apical cells with numerous phenolics. At later developmental stages and during secondary wall thickening, phenolics are transferred to the cell walls of the trichomes. Due to the diffuse deposition of phenolics in the cell walls, trichomes provide protection against UV-B radiation by behaving as optical filters, screening out wavelengths that could damage sensitive tissues. Protection from strong visible radiation is also afford by increased surface light reflectance. Moreover, the mixtures of trichome phenolics represent a superficial chemical barrier that provides protection against biotic stress factors such as herbivores and pathogens. Although the cells of some trichomes die at maturity, they can modulate their quantitative and qualitative characteristics during development, depending on the prevailing conditions of the external biotic or abiotic environment (Karabourniotis *et al.*, 2020). In fact, the structure and chemical constituents of trichomes may change due to the particular light regime, herbivore damage, wounding, water stress, salinity and the presence of heavy metals. Hence, trichomes represent dynamic protective structures that may greatly affect the outcome of many plant environment interactions (Fig. 3).

In the future, detailed knowledge on the biology of plant glandular trichome development and metabolism will generate new leads to tap the largely unexploited potential of glandular trichomes in plant resistance to pests and lead to the improved production of specialized metabolites with high industrial or pharmacological value. Due to the secretory potential, the glandular trichomes are of great scientific and with practical significance. Our understanding of the developmental process of glandular trichomes is limited, and no single plant species serves as a unique model. Understanding the molecular basis of
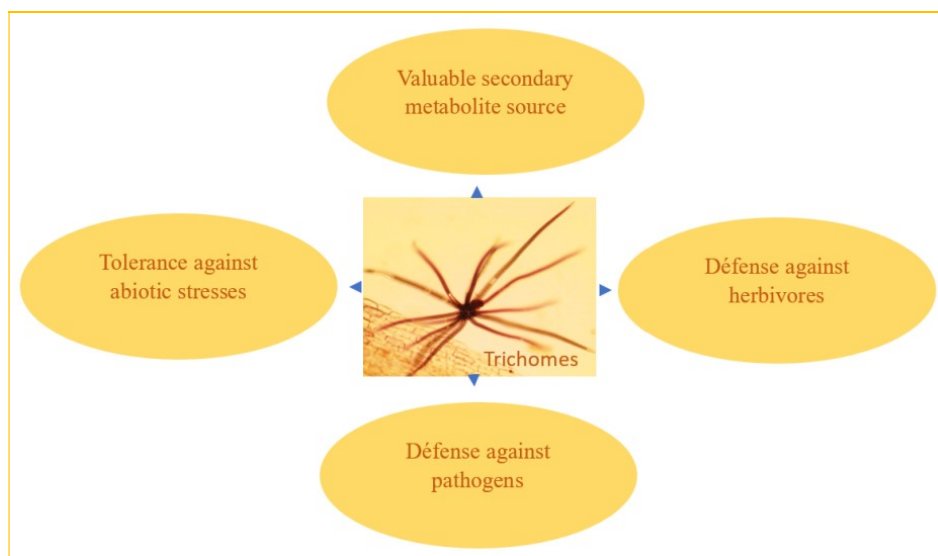

Fig. 3: Significant role of plant epidermal trichomes for better development of agriculture

glandular trichome development and specialized metabolites not only offers useful avenues for research in plant breeding that will lead to the improved production of desirable metabolites, but also provides insights for plant epidermal development research.

CONCLUSION

The diversely distributed non-glandular or glandular trichomes can be considered as an important plant tool of defense against herbivorous insects, pathogens and abiotic stresses, in addition to the taxonomic key construction. Most of the trichome induced metabolic compounds play significant role in medicinal industry now. Due to the reason, the discovery and study on molecular mechanism of genes regarding thetrichome metabolite production are essential for progression of future life. However, the full potential of trichomes has not been exploited due to the incomplete knowledge regarding complex glandular secondary metabolism. Through breeding or genetic engineering by using trichome specific promoters, we can develop a stronger grip on how to obtain the desired levels of biocides in a tissue-specific manner. Similarly, the identification of stress tolerant glandular genome may be a reason for transgenic production of abiotic or biotic stress tolerant plants in the future agricultural scenario.

REFERENCES

Adebooye, O.C., Hunsche, M., Noga, G. & Lankes, C. (2012). Morphology and density of trichomes and stomata of *Trichosanthes cucumerina* (Cucurbitaceae) as affected by leaf age and salinity. *Turkish Journal of Botany* 36(4): 328-335.

Adedeji, O. & Jewoola, O.A. (2008). Importance of leaf epidermal characters in the Asteraceae family. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 36(2): 7.

Ali, M.A. & Al-Hemaid, F.M. (2011). Taxonomic significance of trichomes micromorphology in cucurbits. *Saudi journal of biological sciences* 18(1): 87-92.

Amrehn, E., Heller, A. & Spring, O. (2014). Capitate glandular trichomes of *Helianthusannuus* (Asteraceae): ultrastructure and cytological development. *Protoplasma* 251: 161-167.

Bar, M. & Shtein, I. (2019). Plant trichomes and the biomechanics of defense in various systems, with Solanaceae as a model. *Botany* 97(12): 651-660.

Bosabalidis, A.M. (1990). Glandular trichomes in *Satureja thymbra* leaves. *Annals of Botany* 65(1): 71-78.

Cardoso, P. H., Salimena, F. R. G., Somavilla, N., Menini Neto, L. & Trovo, M. (2023). Verbenaceae from the Serra do Cipo, Minas Gerais, Brazil: Recognition of the New and Rare *Stachytarpheta odorata* and an Update of the Species Richness. *Tropical Plant Biology* 16(3): 123-134.

Chwil, M. & Kostryco, M. (2020). Histochemical assays of secretory trichomes and the structure and content of mineral nutrients in *Rubus idaeus* L. leaves. *Protoplasma* 257(1): 119-139.

Combrinck, S., Du Plooy, G.W., McCrindle, R.I. & Botha, B.M. (2007). Morphology

and histochemistry of the glandular trichomes of *Lippias caberrima* (Verbenaceae). *Annals of botany* 99(6): 1111-1119.

Fahn, A. (1986). Structural and functional properties of trichomes of xeromorphic leaves. *Annals of Botany* 57(5): 631-637.

Janosevic, D., Budimir, S., Alimpic, A., Marin, P., Al, S.N., Giweli, A. & Duletic-Lausevic, S. (2016). Micromorphology and histochemistry of leaf trichomes of *Salvia aegyptiaca* (Lamiaceae). *Archives of Biological Sciences* 68(2): 291-301.

Kahraman, A., Celep, F. & Dogan, M. (2010). Anatomy, trichome morphology and palynology of *Salvia chrysophylla* Stapf (Lamiaceae). *South African Journal of Botany* 76(2): 187-195.

Karabourniotis, G., Liakopoulos, G., Nikolopoulos, D. & Bresta, P. (2020). Protective and defensive roles of non-glandular trichomes against multiple stresses: structure–function coordination. *Journal of Forestry Research* 31(1): 1-12.

Kaur, S., Khanal, N., Dearth, R. & Kariyat, R. (2023). Morphological characterization of intraspecific variation for trichome traits in tomato (*Solanum lycopersicum*). *Botanical Studies* 64(1): 1-17.

Kennedy, G.G. (2003). Tomato, pests, parasitoids, and predators: tritrophic interactions involving the genus Lycopersicon. *Annual review of entomology* 48(1): 51-72.

Kolb, D. & Müller, M. (2004). Light, conventional and environmental scanning electron microscopy of the trichomes of *Cucurbita pepo* sub sp. pepo var. styriaca and histochemistry of glandular secretory products. *Annals of Botany* 94(4): 515-526.

Kowalski, R., Kowalska, G., Jankowska, M., Nawrocka, A., Kałwa, K., Pankiewicz, U. & Włodarczyk-Stasiak, M. (2019). Secretory structures and essential oil composition of selected industrial species of Lamiaceae. *Acta Scientiarum Polonorum Hortorum Cultus* 18(2): 53-69.

Liu, J., Xia, K.F., Zhu, J.C., Deng, Y.G., Huang, X.L., Hu, B.L. & Xu, Z.F. (2006). The nightshade proteinase inhibitor IIb gene is constitutively expressed in glandular trichomes. *Plant and Cell Physiology* 47(9): 1274-1284.

Mahlberg, P.G. & Kim, E.S. (2004). Accumulation of cannabinoids in glandular trichomes of Cannabis (Cannabaceae). *Journal of Industrial Hemp* 9(1): 15-36.

Mahmoud, S.S., Maddock, S. & Adal, A.M. (2021). Isoprenoid metabolism and engineering in glandular trichomes of Lamiaceae. *Frontiers in Plant Science* 12: 699157.

Marchica, A., Ascrizzi, R., Flamini, G., Cotrozzi, L., Tonelli, M., Lorenzini, G. & Pellegrini, E. (2021). Ozone as eustress for enhancing secondary metabolites and bioactive properties in *Salvia officinalis*. *Industrial Crops and Products* 170: 113730.

Matos, E.C. & Paiva, É.A.S. (2012). Structure, function and secretory products of the peltate glands of *Centrolobium tomentosum* (Fabaceae, Faboideae). *Australian Journal of Botany* 60(4): 301-309.

Modenesi, P., Serrato-Valenti, G. & Bruni, A. (1984). Development and secretion of clubbed trichomes in *Thymus vulgaris* L. *Flora* 175(3): 211-219.

Mota, L., Figueiredo, A.C., Pedro, L.G., Barroso, J.G. & Ascensao, L. (2013). Glandular trichomes, histochemical localization of secretion, and essential oil composition in *Plectranthus grandidentatus* growing in Portugal. *Flavour and Fragrance Journal* 28(6): 393-401.

Muravnik, L.E. (2021). The structural peculiarities of the leaf glandular trichomes: A review. *Plant Cell and Tissue Differentiation and Secondary Metabolites: Fundamentals and Applications* 63-97.

Muravnik, L.E., Kostina, O.V. & Shavarda, A.L. (2016). Glandular trichomes of *Tussilago farfara* (Senecioneae, Asteraceae). *Planta* 244: 737-752.

Naidoo, Y., Kasim, N., Heneidak, S., Nicholas, A. & Naidoo, G. (2013). Foliar secretory trichomes of *Ocimum obovatum* (Lamiaceae): micromorphological structure and histochemistry. *Plant Systematics and Evolution* 299: 873-885.

Passos, J.L., Meira, R.M.S.A. & Barbosa, L.C.A. (2009). Foliar anatomy of the species *Lantana camara* and *L. radula* (Verbenaceae). *Planta Daninha* 27: 689-700.

Ramirez, A.M., Saillard, N., Yang, T., Franssen, M.C., Bouwmeester, H.J. & Jongsma, M.A. (2013). Biosynthesis of sesquiterpene lactones in pyrethrum (*Tanacetum cinerariifolium*). *PloS one* 8(5): e65030.

Raseena, N.R. & Beevy, S.S. (2018). Morphology, structure and distribution of floral trichomes in *Coccinia grandis* (L.) voigt. (Cucurbitaceae). *International Journal of Agriculture, Environment and Biotechnology* 11(3): 507-515.

Shafira, S. & Salamah, A. (2020). Analysis of leaves trichomes of *Eclipta prostrata*, *Eleutheranthera ruderalis*, *Synedrella nodiflora*, and *Tridax procumbens* (Asteraceae, Heliantheae). In *IOP Conference Series: Earth and Environmental Science* 524 (1): 012001. IOP Publishing.

Silva, B.D., Aschenbrenner, A.K., Lopes, N.P. & Spring, O. (2017). Direct analyses of secondary metabolites by mass spectrometry imaging (MSI) from sunflower (*Helianthus annuus* L.) trichomes. *Molecules* 22(5): 774.

Singini, E.J., Nuapia, Y., Chimuka, L. & Risenga, I.M. (2023). The effect of elevated temperatures on trichomes, essential oil composition and yield of *Lippia javanica*: A chemometric approach. *South African Journal of Science* 119(1-2): 1-6.

Song, Z., Wang, P., Chen, X., Peng, Y., Cai, B., Song, J. & Zhang, H. (2022). Melatonin alleviates cadmium toxicity and abiotic stress by promoting glandular trichome development and antioxidant capacity in *Nicotiana tabacum*. *Ecotoxicology and Environmental Safety* 236: 113437.

Sun, M., Zhang, Y., Zhu, L., Liu, N., Bai, H., Sun, G. & Shi, L. (2022). Chromosome-level assembly and analysis of the Thymus genome provide insights into glandular secretory trichome formation and monoterpenoid biosynthesis in thyme. *Plant Communications* 3(6).

Taleb-Contini, S. H., Schorr, K., Costa, F. B. D. & Oliveira, D. C. R. D. (2007). Detection of flavonoids in glandular trichomes of *Chromolaena* species (Eupatorieae, Asteraceae) by reversed-phase high-performance liquid chromatography. *Revista Brasileira de Ciencias Farmaceuticas* 43: 315-321.

Tan, J., Walford, S.A., Dennis, E.S. & Llewellyn, D. (2016). Trichomes control flower bud shape by linking together young petals. *Nature Plants* 2(7): 1-5.

Tian, N., Liu, F., Wang, P., Zhang, X., Li, X. & Wu, G. (2017). The molecular basis of glandular trichome development and secondary metabolism in plants. *Plant Gene*, *12*, 1-12.

Wagner G.J., Wang E., Shepherd R.W. (2004). New approaches for studying and exploiting an old protuberance, the plant trichome. *Annals of Botany* 93(1):3–11.

Wagner, G. J. (1991). Secreting glandular trichomes: more than just hairs. *Plant Physiology* 96(3): 675-679.

Wang, X., Shen, C., Meng, P., Tan, G. & Lv, L. (2021). Analysis and review of trichomes in plants. *BMC plant biology* 21(1): 1-11.

Werker, E. & Fahn, A.N.D.A. (1981). Secretory hairs of *Inula viscosa* (L.) Ait. Development, ultrastructure, and secretion. *Botanical Gazette* 142(4): 461-476.

Zhang, H., Liu, P., Wang, B. & Yuan, F. (2021). The roles of trichome development genes in stress resistance. *Plant Growth Regulation* 95(2): 137-148.

Zhigila, D.A., Sawa, F.B.J., Aluko, T.A., Oladele, F.A. & Rahaman, A.A. (2015). Leaf epidermal anatomy in five varieties of *Capsicum annuum* L. Solanaceae. *American Journal of Experimental Agriculture* 5(4): 392.

Zuzarte, M.R., Dinis, A.M., Cavaleiro, C., Salgueiro, L.R. & Canhoto, J.M. (2010). Trichomes, essential oils and in vitro propagation of *Lavandula pedunculata* (Lamiaceae). *Industrial Crops and Products* 32(3): 580-587.