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A comprehensive review on glandular trichomes, gene regulating trichome development and how can we apply gene editing technologies to develop a specific type of trichome type

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Abstract
Trichomes are unicellular or multicellular appendages that extend from the aboveground epidermal cells of plants. These solitary or multicellular epidermal projections are present on the aerial portions of plants and serve a variety of biological functions, including protecting the plant from water loss, ultraviolet (UV) radiation, and herbivore attacks. By reducing excessive transpiration, providing defence against insect predation, and shielding plants from harmful UV light, trichomes play a crucial role in enhancing plant tolerance to both biotic and abiotic stresses. The density and shape of trichomes vary widely across species, displaying structural modifications that correspond to their specific functions. In addition to their protective roles, trichomes can manufacture specialized metabolites, undergo physiological changes, and assist in detoxification by accumulating harmful substances Tomato plants possess seven different types of trichomes, which are classified as either glandular or non-glandular. Among these, glandular trichomes are the most prevalent on tomato leaves and stems. Glandular trichomes (GTs) are epidermal outgrowths capable of biosynthesizing and secreting specialized compounds, making them highly significant from both scientific and practical perspectives. They contribute substantially to herbivore resistance, a characteristic particularly important for wild tomato species. One specific type found on tomato leaves is the type-IV glandular trichome (GT), which plays a key role in plant defence and metabolic processes.

Keywords: Trichomes, glandular trichomes, genes, *Agrobacterium tumefaciens*, biotic and abiotic

Introduction
Tomatoes (*Solanum lycopersicum* L.) are among the most essential vegetable crops globally. They rank as the second most cultivated vegetable in terms of both production and consumption. In recent years, demand for tomatoes has surged due to their rich content of nutritionally valuable carotenoids, fibres, vitamins, and minerals (Amr & Raie, 2022) [2]. Tomatoes are also rich in antioxidants, including beta-carotene, as well as various phenolic compounds such as flavonoids, hydroxycinnamic acid, chlorogenic acid, homovanillic acid, and ferulic acid (Collins *et al*., 2022) [9]. Terrestrial plants, being anchored in the soil, must continuously adapt to their dynamic and complex environments as they grow and develop (Dahl & Arens, 2020) [10]. One significant adaptation that emerged when plants transitioned from aquatic to terrestrial habitats was the development of epidermal hair-like structures. These specialized structures played a crucial role in helping plants cope with the challenges of land environments, such as water retention, protection from herbivores, and resistance to environmental stressors (Huegel, 2019) [28]. When these structures are present on a plant's aerial organs, they are referred to as trichomes, whereas those found on underground parts are known as root hairs (Doroshkov *et al*., 2019) [15]. In plants, trichomes are hair-like appendages that emerge from the above-ground epidermal cells and can be either unicellular or multicellular (X. Wang *et al*., 2021) [67]. Trichomes serve as a protective barrier, defending plants against diseases, herbivores, UV radiation, excessive water loss, and also aiding in seed protection and dispersal (Dhankhar *et al*., 2023) [14]. Although trichomes are small, they play a crucial role in both plant health by producing terpenoids (Glas *et al*., 2012) [23]. Tomato plants have seven distinct types of

trichomes, which are classified as either glandular or non-glandular (Kaur *et al.*, 2023) [33]. Trichomes are generally categorized based on their structure and function, classifying them as unicellular or multicellular, branched or unbranched, and glandular or non-glandular (Deepa, 2024) [12]. Trichomes also divided into various parts, such as head, star, hook, and scale. Glandular trichomes are usually present in all or part of the subepidermal tissue on the leaf surface (Muravnik, 2020) [45]. The growth of plant trichomes is regulated and coordinated by multiple factors, including environmental conditions, hormonal signals, regulatory genes, and non-coding RNA. These elements work together to influence trichome development, ensuring that plants can adapt to their surroundings and effectively perform their protective and physiological functions (Fambrini & Pugliesi, 2019) [18]. Among these factors, regulatory genes, which include transcription factors and functional genes, play a crucial role in controlling the initiation, growth, and development of trichomes (Wang *et al*, 2021) [67].

Glandular trichomes

Glandular trichomes, specialized structures formed from plant epidermal cells, serve a variety of biological functions depending on the plant species (Schuurink & Tissier, 2020) [54]. The glandular trichomes are of 4 types based on shape and function (Bergau *et al*., 2015) [3]. Type 1 trichome capitate is large and has multicellular stalk and a glandular head (Uzelac *et al*., 2019) [61]. Type IV trichome (Peltate) is short stalked with a broad, and has multicellular glandular head (Deepa, 2024) [12]. Type VI trichome is capitate is the most abundant glandular type in most of the cultivated tomato variety. Type VII trichome is small capitate trichome is similar to type VI but with a smaller glandular head (Bergau *et al*., 2015; Guo *et al*., 2013) [3, 24]. These functions include providing biochemical protection through the secretion of secondary metabolites and offering mechanical defence due to their physical characteristics (Tian *et al*., 2017) [58]. Glandular trichomes (GT) have attracted significant attention due to their potential to produce a wide variety of specialized plant metabolites (Tsugawa *et al*., 2021) [60]. Trichomes, present in many angiosperms as well as in numerous gymnosperms and bryophytes, are classified into two types: secretory glandular trichomes (glandular trichomes) and non-secretory glandular trichomes (non-glandular trichomes) (Han *et al*., 2022) [25]. Secretory or glandular trichomes produce and secrete secondary metabolites, including terpenes, acyl sugars, and phenolic compounds, which provide chemical defence against herbivores and pathogens (Al-Khayri *et al*., 2023) [1]. Glandular trichomes also provides defence against biotic and abiotic stresses (Kundan *et al*., 2019) [40]. Non-glandular or non-secretory trichomes do not secrete substances but serve as physical barriers against biotic and abiotic stress factors (Zhang *et al*, 2021) [76].

Role of glandular trichomes in abiotic stress tolerance in tomato

Unfavourable environmental conditions, including biotic and abiotic stress, can inhibit plant growth, development, and reproduction (Chaudhry & Sidhu, 2022) [7]. Biotic stress responses in plants can be triggered by various factors, including insects, other herbivores, viruses, and microbes. In contrast, abiotic stressors encompass environmental conditions such as UV radiation, heavy metals, extreme temperatures (cold and heat), salinity, and drought (Jan *et al*., 2021) [29]. The glandular trichomes secrete substances like polyphenols or acyl sugars, which can trap insects and lead to their ingestion of toxins or cause them to choke to death (F. Wang *et al*., 2022) [65]. UV-B radiation stimulates the expression of the trichome-initiation gene GL3, leading to an increased density of leaf trichomes, which helps reflect more light and reduce transpiration (Rai & Agrawal, 2023) [50]. Trichomes play a crucial role in protecting plants from UV-B radiation. Mutants with a higher number of trichomes than the wild type show increased resistance to UV-B, while mutants with fewer trichomes are more susceptible to UV-B damage (Karabourniotis *et al*., 2020) [31]. Additionally, plants with lower densities of glandular trichomes are more susceptible to ozone stress and the damaging effects of ozone compared to the wild type (Nowroz *et al*., 2023) [47]. Glandular trichomes on the leaf surface act as chemical barriers, neutralizing ozone before it can reach the leaf. This function plays a vital role in reducing ozone toxicity. Therefore, in polluted environments, the presence of leaf trichomes may be a critical factor influencing the distribution of species (Lihavainen *et al*., 2017; Nowroz *et al*., 2023) [43, 47]. In addition, glandular trichomes help protect plants from the damaging effects of drought and high temperatures (Zhang *et al*., 2021) [76]. The ability of tomatoes to endure stress is closely linked to the density and types of trichomes present on the plant (Kariyat, 2020) [32].

In tomato plants, glandular trichomes are associated with the production of both volatile and non-volatile secondary metabolites, such as flavonoids, acyl sugars, terpenoids, and phenylpropanoids (Liu *et al*., 2019) [44]. Allelochemicals present in the glandular trichomes of wild tomato species are diverse and believed to contribute to pest resistance. The three most recognized and likely the most studied groups of these compounds are methyl ketones, sesquiterpenes, and acyl sugars (Labate *et al*., 2007) [41]. Although research on tomatoes has primarily focused on Hemiptera and Lepidoptera as the main pests, it has been shown that glandular trichomes in wild tomato varieties also provide resistance to other pest taxa (Rakha *et al*., 2017) [52]. Tomato plants with high densities of glandular trichomes, specifically types IV and VI, exhibit strong resistance to arthropods. This resistance is largely attributed to the presence of allelochemicals, which primarily include tridecanones (methylketones), sesquiterpenes (terpenoids), and acyl sugars. These chemical compounds play a crucial role in deterring herbivorous insects and enhancing the plant's natural defense mechanisms (Escobar-Bravo *et al*., 2018; Rakha *et al*., 2017) [16, 52]. Trichomes serve as a natural defense mechanism by hindering insect movement and preventing them from biting the plant (Despland, 2019; Watts & Kariyat, 2022) [13, 68]. Additionally, tomato glandular trichomes detect insect movement and act as mechanoreceptors, initiating internal responses such as the production of jasmonic acid (JA) and salicylic acid (SA) (Zhang *et al*., 2021) [76]. The insect becomes trapped in the secretions of glandular trichomes, which produce acyl sugars or polyphenols, forcing it to ingest toxins or suffocate, ultimately leading to its death (NANDI *et al*., 2022) [46]. However, glandular trichomes can also detect the physical movements of insects and act as mechanoreceptors, triggering internal processes such as the production of jasmonic acid (JA) and salicylic acid (SA) (Zhang *et al*., 2021) [76]. *Solanum habrochaites* is one of the most extensively studied wild tomato species for its resistance to arthropods (de Oliveira *et al*., 2020) [11]. Type IV and VI trichomes in this widely distributed species have demonstrated resistance to more thrips species and aphid species (Blanco-sanchez *et al*, 2021). Among these, only one entry, PI 134417, has been identified *Solanum habrochaites* var. Glabratum exhibits resistance to several pests (Savi, 2022) [53].

Gene regulating trichome development in tomato plant

Glandular trichomes are essential for tomatoes to defend against herbivores (Tabary *et al*., 2024) [57]. *Artemisia annua* and tomatoes have both been previously proposed as suitable models for studying the formation of glandular trichomes (Qin *et al*., 2021) [49]. In *Artemisia annua* and tomatoes, several transcription factors involved in glandular trichome initiation have been identified, with most belonging to the R2R3-MYB and HD-ZIP IV transcription factor subfamilies. Additionally, certain members of the R2R3-MYB subfamily have been shown to regulate specialized metabolism (R. A. Khan *et al*., 2021) [36]. R2R3-MYB, along with MIXTA and MIXTA-like genes, play a crucial role in determining the fate of epidermal cells (B. Xu *et al*., 2021) [71]. The first MIXTA gene was identified in Snapdragon (*Antirrhinum majus*), where it regulates the differentiation of conical epidermal cells from flat epidermal cells (Qiao *et al*., 2023) [48]. In tomatoes and *Artemisia annua*, three members of the R2R3-MYB subfamily have been identified as positive regulators of glandular trichome initiation, including SlMX1 in tomatoes (Ewas *et al*., 2022) [17], and AaMYB1 and AaMIXTA1 in *Artemisia annua* (Chalvin *et al*., 2019) [6]. Plants of *Artemisia annua* that overexpress AaMYB1 have been shown to develop a higher density of glandular trichomes (Li *et al*., 2024) [42]. Additionally, SlMX1 in tomatoes and AaMIXTA1 in *Artemisia annua* are downregulated (Han *et al*., 2022). A decrease in the expression of these genes reduces the density of glandular trichomes, whereas their overexpression increases it. While AaMYB1 belongs to a distinct lineage within the R2R3-MYB subfamily, both AaMIXTA1 and SlMX1 are classified as MIXTA-like genes (Yuan *et al*., 2023) [75]. Members of the HD-ZIP IV subfamily of transcription factors are known to play a crucial role in the differentiation of plant epidermal cells, contributing to cuticle biosynthesis as well as the patterning of trichomes and stomata (Zhang *et al*., 2019) [77]. Recent studies have shown that the HD-ZIP IV transcription factors AaHD1 and AaHD8 play a positive role in initiating glandular trichome development in *Artemisia annua* (Kovalchuk *et al*., 2019) [39]. Overexpression of either AaHD1 or AaHD8 results in an increase in glandular trichome density, while downregulation of both genes has the reverse effect (Fu *et al*., 2024) [21]. In tomatoes, AaHD8 acts upstream of AaHD1 to directly stimulate its expression (Hua, Chang, Xu, *et al*., 2021) [26, 71]. The closest homolog of AaHD8 in tomatoes is CUTIN DEFICIENT 2 (SlCD2) (Berhin *et al*., 2022) [4]. Due to a loss-of-function mutation in SlCD2, the tomato sticky peel mutant has less glandular trichomes, especially type VI (Vendemiatti, 2020) [62]. Therefore, it seems that AaHD8/SlCD2 plays a similar role in the positive regulation of glandular trichome initiation in *Artemisia annua* and tomatoes. Another HD-ZIP IV transcription factor, WOOLLY (Wo), appears to be a crucial regulator of tomato glandular trichome initiation (Wu *et al*., 2023) [69]. Dominant point mutations in the C-terminus region of Wo induce the phenotypic of woolly mutants, which show noticeably greater trichome density in tomato plants (Yang *et al*., 2011) [73]. Given that type I glandular trichome density in tomatoes is lower in Wo-RNAi plants and higher in plants with dominant woolly mutations, the preliminary characterisation of Wo suggests that Wo stimulates type I glandular trichome initiation (Yu *et al*., 2024) [74]. However, a recent reanalysis of the phenotypic of woolly mutants shows that the type III and type V non-glandular trichome densities are larger and the type IV glandular trichome density is lower in tomato mature leaves (Gasparini *et al*., 2023) [22]. Two other transcription factors that are crucial for glandular trichome initiation but do not fall under the R2R3-MYB or HD-ZIP IV subfamilies have also been discovered in recent studies in tomatoes: The zinc-finger proteins MYELOCYTOMATOSIS-RELATED 1 (SlMYC1), a bHLH protein, and HAIR (SlH) C2H2 (Shvachko *et al*., 2020) [55]. RNAi-induced downregulation of SlMYC1 or missense mutations in SlH, respectively, reduce the density of type VI or type I glandular trichomes in tomatoes (Fonseca *et al*., 2022) [20]. Furthermore, SlH knockout produces a phenotype without hair, whereas myc1 knockout mutants in tomatoes lack type VI glandular trichomes (J. Xu *et al*., 2018) [72].

These results imply that SlMYC1 positively regulates the onset of type VI glandular trichomes in tomato plants and that SlH is an essential positive regulator of the commencement of all glandular trichome types (J. Xu *et al*., 2018) [72]. SlMYC1 is also a major regulator of later phases of tomato type VI glandular trichome morphogenesis, as evidenced by the interesting fact that SlMYC1 RNAi plants have smaller glands and shorter stalks in type VI glandular trichomes (J. Xu *et al*., 2018) [72].

Table 1: Describing the genes involved in glandular trichome development in tomato plants.

S. No	Gene	Function	Reference
1	SlMYC1	Essential for type VI glandular trichome development; its knockdown leads to smaller type VI trichomes.	(J. Xu *et al*., 2018) [72]
2	Woolly (Wo)	A homeodomain protein that mediates jasmonic acid signaling, influencing trichome initiation.	(Hua, Chang, Wu, *et al*., 2021) [27]
3	SlCycB2	A cyclin that interacts with Woolly to regulate type I trichome density.	(Feng *et al*., 2021) [19]
4	HAIRPLUS (HAP)	A gene involved in epigenomic modifications affecting glandular trichome density.	(Fonseca *et al*., 2022) [20]
5	SlTRY	Have negative impact on glandular trichome development in tomato plant.	(Tominaga-Wada *et al*., 2013) [59]

Techniques that can apply to tomato plant to develop specific type of trichome

A potent genome-editing technique called CRISPR-Cas9 can be used to create particular types of trichomes (Zlobin *et al*., 2020) [78]. CRISPR/Cas has dominated the area of genome editing in recent years due to its ease of use, adaptability, durability, and affordability (Wan *et al*., 2019) [64]. In order to address global climate change and other agricultural, environmental, and ecological concerns, its use in crop development is particularly important (M. D. Khan *et al*., 2023) [35]. Scientists have created a variety of CRISPR/Cas toolboxes that allow for precise genome changes, such as base editing, transcriptome regulation, epigenome editing, targeted mutagenesis at loci, and the exact replacement or tagging of genes and alleles in plants (Villiger *et al*., 2024) [63]. Two vectors, p2gR-TRI-A and p2gR-TRI-B, each carrying two gRNAs that targeted three genes linked to trichome formation, were used to alter tomatoes (Soda *et al*., 2018) [56]. Both vectors include the same gRNA (T2-ETC2), which targets ETC2 and maybe CPC, a far less desired target. The vectors also include distinct gRNAs (T1A-TC or T1B-TC) (Xing *et al*., 2014) [70]. In contrast to T1B-TC, T1A-TC's 18-bp target sequence is complimentary. Both T1A-TC and T1B-TC target two genes: TRY and CPC. While there are two mismatches between T1B-TC and CPC, there is only one between T1A-TC gRNA's 20-nt target and either TRY or CPC, and between T1B-TC and TRY. Approximately 70% of the T1 transgenic plants for p2gR-TRI-A had densely clustered trichomes, as expected for try cpc double or try cpc etc2 triple mutant plants (Kirik *et al*., 2004) [37]. Additionally, Crisper-cas 9 can control the synthesis of phytohormones that trigger the formation of particular trichomes (Rajput *et al*., 2021) [51].

Using of *Agrobacterium tumefaciens* in producing glandular trichomes in tomato plants

To improve glandular trichome production and function, tomato plants are genetically modified using Agrobacterium tumefaciens (Kortbeek *et al*., 2016) [38]. The particular gene that produces glandular trichomes is included into A. tumefaciens' t-DNA (Chen *et al*., 2018) [8]. Genes involved in trichome initiation and development include WAX2, HD-Zip IV, and MIXTA-like (L. Wang *et al*., 2020) [66]. Under the guidance of an appropriate promoter, such as the 35S CaMV promoter for constitutive expression or glandular trichome-specific promoters like AAT1 or GPAT1, the chosen genes are cloned into a T-DNA section of a binary vector. Agrobacterium tumefaciens strains such as LBA4404 and GV3101 are exposed to the vector by heat shock or electroporation (Jeong *et al*., 2024) [30]. Agrobacterium suspension with the recombinant vector infects tomato explants (cotyledons, hypocotyls, or leaves) (Khamis *et al*., 2024) [34]. These genes are integrated into A. tumefaciens' t-DNA, which is then transferred to tomato plants. The bacteria target the DNA of the plants and produce glandular trichomes as a result (Brencic & Winans, 2005) [5].

Conclusion

Trichomes are the hairlike structures that are formed on the stems, leaves, buds and other parts of the tomato plant. Mostly the trichomes are of two types glandular and non-glandular. These trichomes protects plant against insects and herbivore animal damage and protects from abiotic stresses and protects from transpiration. Plant trichome growth is controlled by environmental factors, hormones, regulatory genes, and non-coding RNA. Glandular trichomes plays a major role in protecting plant from herbivorous animals. The glandular trichome of type IV and type VI gives protection arthropod insects. These trichomes also protects plant from harmful UV-B rays. The glandular trichome development is regulated by 5 major genes like SlMYC1, Woolly (Wo), SlCycB2, HAIRPLUS (HAP), and SITRY. The techniques like Crisper cas9 and *Agrobacterium tumefaciens* are used to induce specific glandular trichomes in tomato plants. The Crisper cas9 uses gene editing, targeted mutagenesis at loci, and the exact replacement or tagging of genes and alleles in plants. By this we can produce glandular trichomes or other trichomes. The *Agrobacterium tumefaciens* use the technique it inserts specific gene. The specific gene inserts into t- DNA of *A tumefaciens* and these bacteria insert into plant's system the bacterium releases the specific gene into plants system and the glandular trichomes are formed. In this way the glandular trichomes playa a major role in protection of plant from various stresses, and these mechanisms are used to produce various types of trichomes in plants.

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