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Tangled in transcription

The web of transcription factors regulating tomato type VI glandular trichome development and specialized metabolites

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Chapter 1

General introduction

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1.1 Plant trichomes

Plant trichomes diversity

The aerial tissues of a plant represent an interface with which a plant interacts with the environment. Plant hairs or trichomes, which are mono- or multicellular protuberances that develop from epidermal cells on aerial tissues, take part in this interaction. Although the name implies that trichomes are shaped like hairs, they vary greatly in morphology, size, density, and distribution (Payne, 1978; Werker, 2000). The frequency and diversity of trichomes found across the whole plant kingdom and their almost ubiquitous presence in angiosperms, testify the selective pressure targeted the development of these structures. It initiated the hypothesis that due to their sessile nature, trichomes are adaptations of plants with crucial ecological significance (H. B. Johnson, 1975). Also for humans plant trichomes have a great importance, with notable examples being the fiber made from trichomes of cotton, artemisinin as the main natural ingredient for malaria treatments, extracted from trichomes of *Artemisia annua*, and cannabinoids, stored in by *Cannabis sativa* trichomes (Wagner et al., 2004). Having seen the diversity of morphologies, the most practical classification of trichomes in use nowadays, although not unambiguous, distinguishes them in non-glandular and glandular types. Because cultivated tomato (*Solanum lycopersicum*) and related wild tomato accessions display eight distinct types of trichomes, both glandular and non-glandular (Channarayappa et al., 1992; Glas et al., 2012; Luckwill, 1943), this species has become an important model crop for studying the developmental and metabolic diversity of trichomes (Feng et al., 2021; Tissier, 2012).

Non-glandular hairy trichomes

The main role of non-glandular trichomes is to act as a physical barrier to protect the plant against biotic and abiotic stresses. For instance, they can reduce mobility, feeding and oviposition of herbivores, influence light absorption and shield from excess of UV radiations, balance loss and uptake of water as well as influencing leaf temperature thus limiting effects of desiccation (Bickford, 2016; Karabourniotis et al., 2020; Levin, 1973; Vermeij, 2015; Wagner et al., 2004). Finally, recent studies revealed an additional role of trichomes as sensors of mechanical stimuli, thus eliciting innate immunity or activate metabolic responses (Matsumura et al., 2022; Sun et al., 2024). Their development has been widely studied in *Arabidopsis*, but the limit of this model plant is that it displays only non-glandular trichomes that are monocellular, branched and polyploid, where the only variation is the number of branches and the density of trichomes.

Glandular trichomes and their specialized metabolites

What all glandular trichomes have in common is that they have one or multiple glands, cells that are capable of producing, storing and secreting metabolites. These glands are supported by a stalk made of one or multiple cells (Payne, 1978). Based on these two defining features, glandular trichomes can be further classified. Peltate trichomes have several glandular cells forming a big head, carried by a short uni- or bicellular stalk. Capitulate trichomes, instead, have a small, unicellular, glandular head with a long and multicellular stalk. Glandular cells of trichomes have a very specialized and highly productive metabolism that make them sinks, which require an intense flux of primary metabolites (Tissier, 2018). In fact, the diversity in this subgroup of plant trichomes is as impressive in the morphology as in the chemical classes of specialized metabolites produced (Schillmiller et al., 2008; Werker, 2000). This variety of compounds constitute a crucial functional adaptation in plants for their interaction with the ecosystem (Lange, 2015). The most abundant metabolite group in trichomes is terpenoids (Glas et al., 2012), which are either exudated as oils or resins (Wagner et al., 2004), or stored in cuticular cavities (J Kortbeek et al., 2023; Lange, 2015; Therezan et al., 2021). They have been found to be important for interactions with arthropods: they can immobilize or act as deterrent against herbivores (Bleeker, Diergaarde, et al., 2011; Bleeker et al., 2012; N. M. Johnson & Baucom, 2024; Kang, Liu, et al., 2010; Kortbeek et al., 2021; Therezan et al., 2021; Xu, 2023), but they can also contribute to attract pollinators (Wagner et al., 2004; Werker, 2000). Another chemical class found in glandular trichomes are phenylpropanoids, among which flavonoids, anthocyanins and lignin

precursors. These compounds can enhance plant defense because they absorb UV light and act as antioxidants or toxic antimicrobials (Agati et al., 2012; Kortbeek, 2022; Landi et al., 2015). Acyl-sugars form another class of specialized metabolites found in trichomes and known to negatively impact insect feeding (Lucini et al., 2015; Mandal et al., 2020; Rakha et al., 2017; Silva et al., 2014; Weinhold & Baldwin, 2011). Compounds from these different classes are found in glandular trichomes of tomato accessions (Ben-Israel et al., 2009; Glas et al., 2012; McDowell et al., 2011; Schillmiller et al., 2010a).

1.2 Tomato type VI glandular trichomes

Tomato has several “hairy” trichomes: Type II, III, V and VIII. Type II and III trichomes are very similar with stalk up to 1 mm long (Figure 1). What distinguish them is the globular base of multiple cells of type II and the single and flat basal cell of type III. However, this difference is often difficult to be observed in practice and these two types are frequently mistaken for one another in literature. A trichome of type V has a short stalk of two or three cells and single flat basal cell. Lastly, type VIII has a thick basal cell and a small unicellular tip.

Tomato has four different types of glandular trichomes: type I, IV, VI and VII (Figure 1). Type I and IV are capitate trichomes that store mostly acyl-sugars. The main difference is that type I has a 2-3 mm long stalk, with a multicellular base and is commonly found among tomato accessions, while type IV is shorter (0.2-0.4 mm) with a single celled flat base and stalk. They are present in adult plants in wild tomatoes accessions or as a juvenile trait in cultivated tomatoes and (Silva et al., 2014; Simmons & Gurr, 2005; Vendemiatti et al., 2017). Type VI and VII are peltate and differentiated by many features. Trichomes type VI, the most abundant on cultivated tomato plants and the main source of terpenes and flavonoids, have a unicellular base and stalk (0.1–0.5 mm long) with four glandular cells supported by a single intermediate cell. Type VII trichomes are much smaller, with a single basal cell, a 0.01–0.1 mm long stalk with 4 to 8 cells glandular head and their specific metabolites content is not completely determined, but includes the alkaloids tomatine and dehydrotomatine (McDowell et al., 2011).

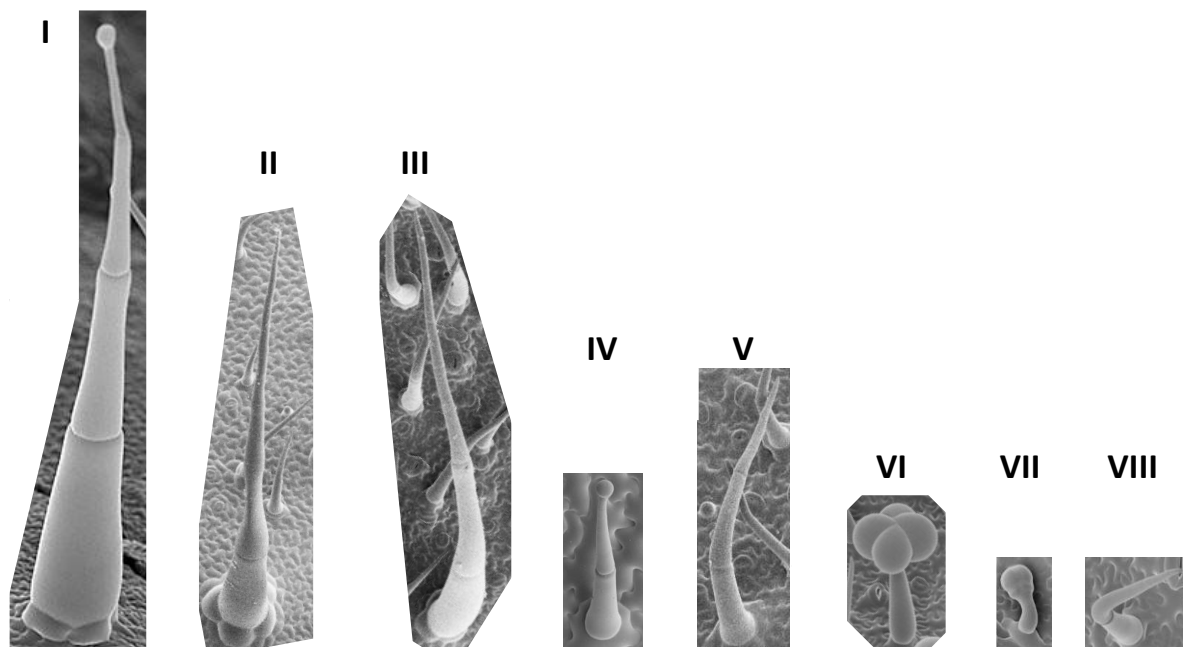


Figure 1 Types of trichomes in tomato accessions. Images of the eight types of trichomes as they appear at the scanning electron microscope. The relative size of the trichome types is not accurate because each type comes from a different image, but it has been made as realistic as possible.

This thesis has focussed on two aspects of trichome biology:

- 1) the production of volatile terpenes in type VI trichomes and
- 2) the regulation of type VI trichome development, with the aim to understand how density and type specificity are realised on tomato leaves and stems.

Regulation of terpene biosynthesis in type VI glandular trichomes

Volatile terpenes, and specifically monoterpenes (C₁₀), sesquiterpenes (C₁₅) and diterpenes (C₂₀), are an important chemical class of specialized metabolites produced by cultivated and wild tomatoes (Falara et al., 2011; Glas et al., 2012; McDowell et al., 2011). In tomato plants, these compounds are synthesized by terpene synthases (TPSs) in the four glandular cells of type VI trichomes and stored in the intercellular cavity between them (Besser et al., 2009; Therezan et al., 2021; Tissier et al., 2017). 52 TPSs genes, of which 34 coding for a functional enzyme, have been identified and characterized in tomato (Bensen & Zeevaart, 1990; Bleeker, Spyropoulou, et al., 2011; Colby et al., 1998; Falara et al., 2011, 2014; Schillmiller et al., 2009, 2010b; van Schie et al., 2007; F. Zhou & Pichersky, 2020). However, our knowledge about how the expression of these genes is controlled and how the biosynthesis of volatile terpenes is regulated in type VI glandular trichomes, is still limited. In the recent years, several studies have identified transcription factors (TFs) that play a role in the transcriptional regulation of TPS genes (Figure 2).

SIMYC1, is a bHLH (basic Helix Loop Helix) TF that, in type VI glandular trichomes on leaves, positively regulates two monoterpene synthase genes (*SITPS5* and *SITPS20*) and two sesquiterpene synthase genes (*SITPS9* and *SITPS12*) (Xu et al., 2018). In type VI trichomes on stems, SIMYC1 positively regulates several monoterpene synthase genes (*SITPS3*, *SITPS5*, *SITPS20* and *SITPS39*) and sesquiterpene synthase genes (*SITPS9*, *SITPS17* and *SITPS31*), but it negatively regulates the sesquiterpene synthase gene *SITPS12* (Xu et al., 2018). The interaction between SIMYC1 and the promoter of *SITPS1*, *SITPS3*, *SITPS5*, *SITPS7*, *SITPS9*, *SITPS12* and *SITPS46* has been confirmed in transactivation assays in *N. bethamiana* (Hua et al., 2020; Spyropoulou et al., 2014b; Xu, 2023).

The TF SIWO (WOOLLY) is a HD-ZIP (Homeodomain Leucine Zipper) type IV TF that, like SIMYC1, can bind *SITPS1*, *SITPS5* and *SITPS12* promoters. For the Jasmonic Acid (JA) induced expression of *SITPS1* and *SITPS5* both SIMYC1 and SIWO are necessary. Because it has been demonstrated that SIMYC1 and SIWO can physically interact, the current hypothesis is that these two TFs form a complex on TPSs promoters and promote their expression, and therefore terpene biosynthesis, in type VI trichome gland cells (Hua et al., 2020; Hua et al., 2021). Because SIJAZ2 (JASMONATE-ZIM-domain), one of the suppressors of the JA signaling pathway, binds both SIWO and SIMYC1 and it impairs their interaction and therefore formation of the modulatory complex, it has been concluded that the induction of terpene biosynthesis by JA occurs via repression of SIJAZ2 (Hua et al., 2020). Also SIJAZ4, SIJAZ6, SIJAZ8 and SIJAZ10 showed *in-vitro* interaction with SIMYC1 (Hua et al., 2020), suggesting that also they could play a role in the regulation of terpene biosynthesis.

SIEOT1 (EXPRESSION OF TERPENOIDS) and its paralog SIEOT2 are two trichome type VI specific transcription factors that also regulate terpene biosynthesis. Both proteins transactivate *in-planta* the promoter of *SITPS5*, coding for a monoterpene synthase, but additionally, SIEOT2 activates the promoter of two sesquiterpene synthase genes, *SITPS17* and *SITPS3*. Accordingly, upregulation of EOT2 resulted in the upregulation of *SITPS3*, *SITPS5*, *SITPS17* and *SITPS31* and in the downregulation of *SITPS39* and *SIEOT1* (Spyropoulou et al., 2014a; Xu, 2023). Similarly to SIEOT1, also SIWRKY73 showed *in-planta* transactivation of the promoter of the trichome-specific *SITPS5* (Spyropoulou et al., 2014b). Another TF expressed specifically in type VI trichomes that is involved in controlling the biosynthesis of terpenes, is SISCL3 (SCARECROW-Like). It acts by activating not only *SITPS5* and *SITPS12* expression, but also many genes involved in the biosynthesis of isoprenoid precursors of terpenes (Yang et al., 2021). SIMYB75 is a negative regulator of terpene biosynthesis, capable of regulating production of sesquiterpenes by binding to the promoter of *SITPS12*, *SITPS31* and *SITPS35* (Gong et al., 2021).

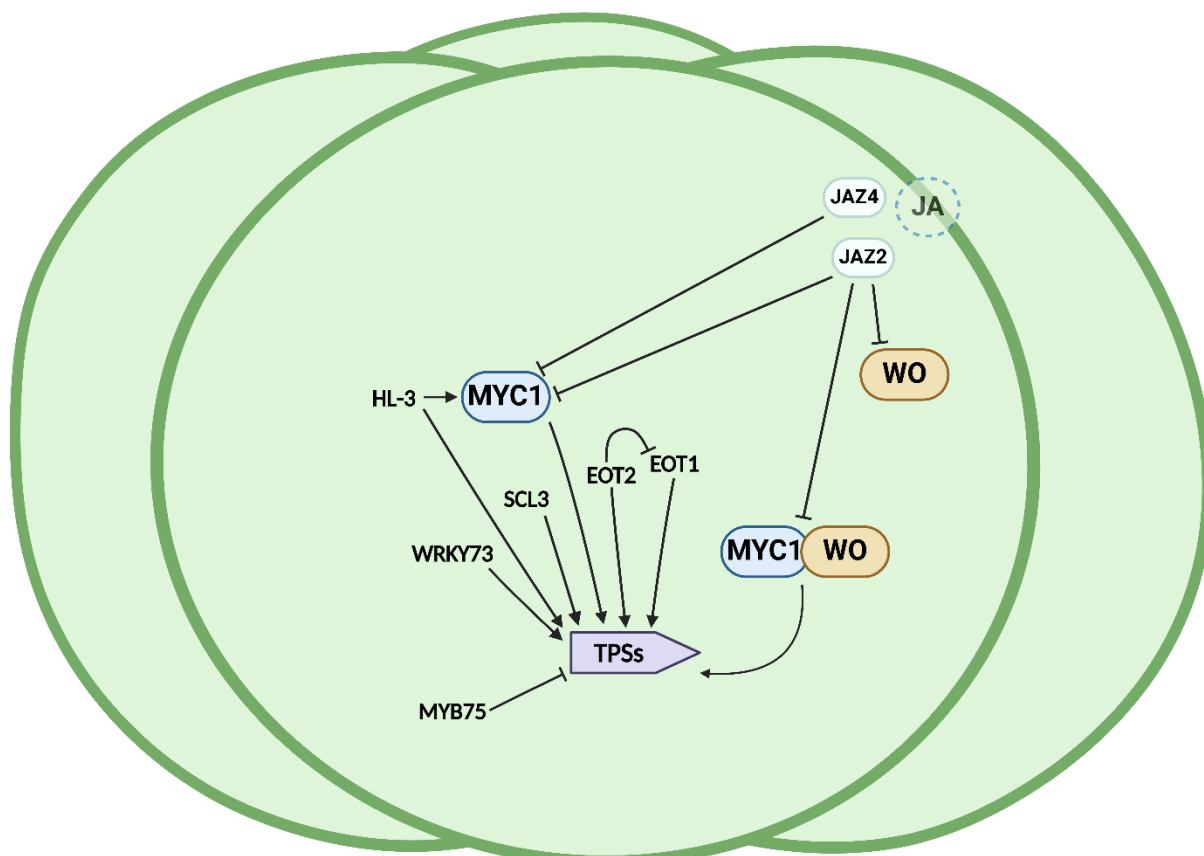


Figure 2 Regulation of type VI trichomes terpene metabolism. Network of transcription factors that are known to control the specialized metabolism of tomato type VI glandular trichomes, mainly involving terpene synthases (TPSs, in purple). The master regulators MYC1 and WO are highlighted with coloured ribbon, including their protein-protein interaction. Circled are also JAZ repressors whose action is dependent from the hormone Jasmonic Acid (JA, in dotted circle).

Regulation of type VI trichomes initiation and development

Most of the current knowledge about the regulation of non-glandular trichomes development comes from studies on the unicellular trichomes of *Arabidopsis thaliana*. With regard to glandular trichomes, many studies have used Tobacco (*Nicotiana tabacum*), *A. annua* and tomato as model plants, mainly because of their specialized metabolism and their relevance in medicine or as defence against herbivores. More recently the development of glandular trichomes has also been investigated in cucumber (*Cucumis sativum*). However, our knowledge about how the development of glandular trichomes unfold and how this process is regulated it is still limited. Nonetheless, in the last decade, many studies have identified TFs involved in the development of glandular trichomes in tomato. This thesis will focus specifically on the development of tomato type VI glandular trichomes (Figure 3).

The first tomato TF with a role in type VI trichome development that was characterized is SIWO (Yang et al., 2011). This HD-ZIP type VI TF has been shown to have a master role in different mechanisms governing the formation of many if not all types of tomato trichomes, including type VI. This function is achieved, besides by direct transcriptional regulation of downstream genes, also by several protein-protein interactions in a dose-dependent manner. SIWO concentration is determined by the balance of self-activation and negative feedback, via the activation of the repressors SIMTR1 and SIMTR2 (MULTICELLULAR TRICHOME REPRESSOR), previously known as SICYCB2 and B3 (Gao et al., 2017; Wu et al., 2023). Both SIMTR1 and SIMTR2 are also regulated by SILN (LANATA), a TF involved in multicellular trichome formation (Xie et al., 2022). SIMTR1 is also regulated by SIGRAS26 (S. Zhou et al., 2018) and bHLH95 (basic HELIX LOOP HELIX; Y. Chen et al., 2020), two TF involved in repression of Gibberellic Acid (GA) signalling. Additionally, *SIWO* expression is influenced by SIGRAS26 (S. Zhou et al., 2018), but this probably occurs indirectly via regulation of SIMTR1. SIMTR1 is the target of regulation by three MYB TFs, SIMYB52, SIMYB75 and SITHM1 (TOMATO HYPOCOTYL MYB). Their

action is controlled by auxin signalling via the ARF (ADP-RIBOSYLATION FACTOR) repressors and both *SITHM1* and *SIMYB75* are expressed in type VI glandular trichomes (Gong et al., 2021; Yuan et al., 2021; Zhang et al., 2015).

The levels of SIWO influence the specification of the developmental fate during the initiation of a trichome. Low concentrations of SIWO result in higher activity of SILFS (LEAFLESS) that induces the development of all glandular trichomes, including type VI. Alternatively, high concentrations of SIWO, result in the expression of SIMX1 and SIWOX3b that, in a complex, repress *SILFS* expression, promoting the formation of non-glandular over glandular trichomes (Wu et al., 2023). SILFS, and therefore gland cells formation, is negatively regulated by two MYB TFs, SIGCR1 and SIGCR2 (GLAND CELL REPRESSOR), by recruiting the repressor SITPL2 (TOPLESS2). The expression of *SIGCR1* and *SIGCR2* is spatiotemporally regulated during trichome development by self-inhibition and repressed by SITOEB1 (TARGET OF EAT b) that is activated by SILFS, forming a negative feedback mechanism (Chang et al., 2024).

SIMYC1 regulates type VI glandular trichome initiation and morphogenesis (Xu et al., 2018). As mentioned before in the context of terpene metabolism regulation, SIWO interacts with SIMYC1 but no evidence yet suggests that the formation of this protein complex is necessary for the regulation of type VI trichome formation. SIWO also interacts with two zinc-finger transcription factor, SIH and SIH2, that interact with each other and are involved in the initiation and elongation of many trichomes types, including glandular type VI, putatively via regulation of SIZFP5 and SIZFP6 (Zinc Finger Protein; Chang et al., 2018; Chun et al., 2021; R. Li et al., 2021; Zheng et al., 2022). Additionally, SIH is also positively regulated by SILN (Xie et al., 2022).

Both SIHL (HAIRLESS) and its homologs SIHL2 and SIHL3 (also named ARPC1), which all are part of the WAVE or ARP2/3 complexes involved in actin nucleation, are involved the initiation and morphogenesis of many tomato trichome types including glandular type VI (Kang et al., 2016; Kang, Shi, et al., 2010; Xie et al., 2020). Interestingly, SIHL3 regulation of trichome density and morphology, could occur via the regulation of *SIMYC1* expression (Chun et al., 2022). SIHL and SIHL2 interact with each other, working together as a complex. Another HD-ZIP type IV TF, SIHD8, can positively regulate the initiation and morphogenesis of many tomato trichome types including glandular types, probably by controlling the expression of *SIH2* and other component of these actin nucleation complexes (Hua et al., 2021; Xie et al., 2020). The initiation and morphogenesis of type VI glandular trichomes is also influenced by a few other TFs, whose connection to the rest of regulatory network is still not understood: the positive regulators SICD2 (CUTIN DEFICIENT) and SIODO-2 (ODORLESS) and the inhibitor SIMIXTA-like (Galdon-Armero et al., 2020; Kang, Liu, et al., 2010; Nadakuduti et al., 2012).

Finally, it is known that JA can have an effect on the initiation of type VI glandular trichomes increasing their density on new leaves (L. Li et al., 2004; Xu et al., 2018; Yan et al., 2013). SIWO, SIMYC1, SIH and SIH2 have all been found to be target of SIJAZ2 repression in absence of JA (Hua et al., 2020, 2022). Additionally, SIJAZ4 targets SIMYC1 and SIHD8 (Hua et al., 2020, 2021). Accordingly, overexpressing JAZ2 or JAZ4 showed to impact trichome density and morphology respectively (Hua et al., 2020; Yu et al., 2018). It seems likely that these two observations are connected, meaning that JA impact on trichome development is probably achieved via JAZ-mediated degradation of known trichome regulators, as already observed for the regulation of terpene metabolism (Hua et al., 2020; Xu, 2023; Xu et al., 2018).

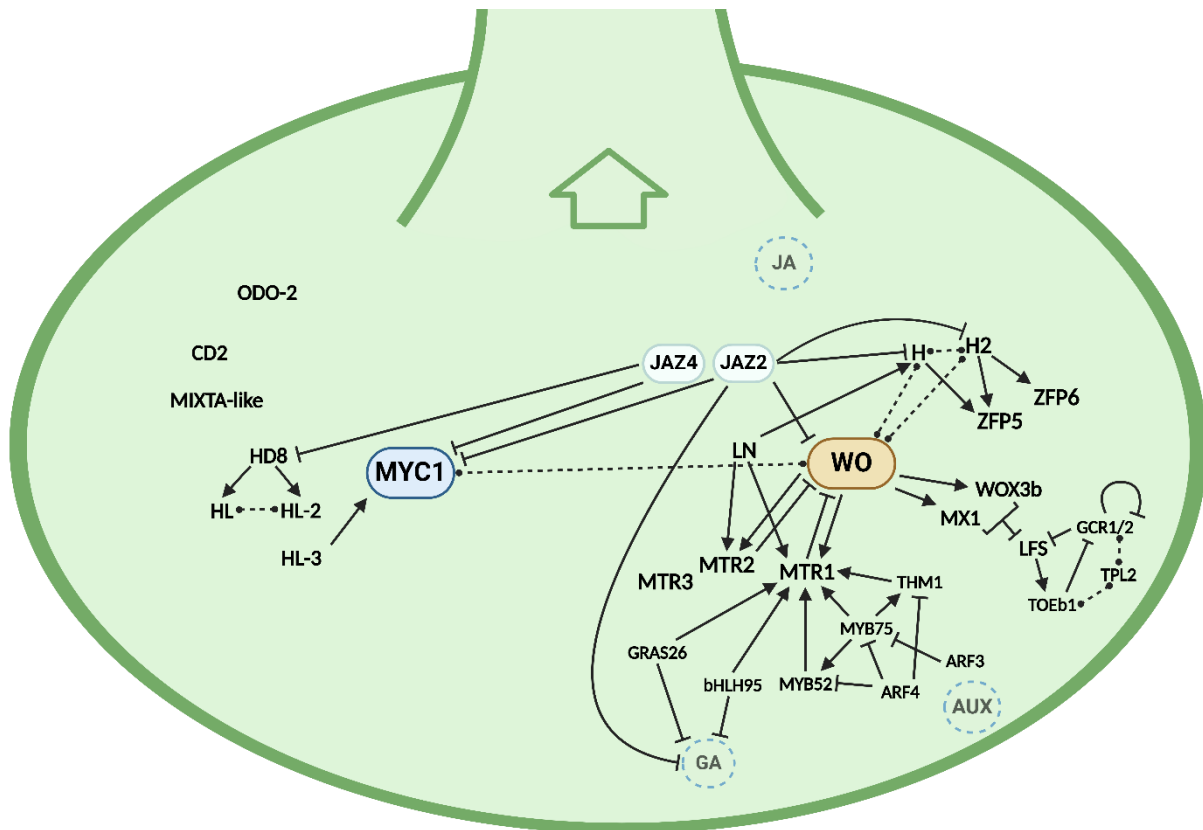


Figure 3 Regulation of type VI trichomes development. A network of transcription factors is known to control the development of type VI glandular trichomes. The master regulators MYC1 and WO are highlighted with coloured boxes. Circled are JAZ repressors JAZ2 and 4 whose action is dependent on the hormone Jasmonic Acid (JA). Highlighted in dotted circles are other two hormones which influence the regulatory network, namely Gibberellic Acid (GA) and Auxin (AUX). Dotted lines represent known protein-protein interactions.

1.3 Thesis outline

This **Chapter 1** introduces plant trichome diversity and ecological importance. Moreover, what is known of the network of tomato transcription factors regulating type VI glandular trichome development and their volatile terpenes specialized metabolism is summarized. Our research aimed to further discover this regulatory network starting from the master regulator SIMYC1.

In **Chapter 2** the regulation of SIMYC1, a key transcription factor regulating type VI glandular trichome development and terpene biosynthesis, was investigated. Using yeast-one-hybrid screening, SlZHD18, a Zinc-finger Homeodomain transcription factor, has been identified as a potential regulator of SIMYC1. Gene silencing (VIGS) and CRISPR knockouts confirmed SlZHD18's role in promoting type VI trichome formation and affecting terpene metabolism. It has also been found that SIMYC1 binds its own promoter, suggesting a possible self-feedback regulatory mechanism.

In **Chapter 3**, the regulatory network of SIMYC1 is investigated by analysing three transgenic lines (MYC1 overexpression, knockdown, knockout). Three candidate transcription factors (SlbHLH114, SIMYB14, and SIWRKY1) likely involved in type VI trichome development and specialized metabolism have been selected and characterized. SlbHLH114 and SIWRKY1 seems to positively regulate trichome density and inhibit volatile terpene production, while SIMYB14 appears less important to these processes. Our results also suggest that SIMYC1 regulation may additionally affect defence responses and primary metabolism.

In **Chapter 4** a tomato mutant line named *glandless* was characterized, with type VI trichomes that lack glandular cells, which resulted in reduced volatile terpene production. Gene mapping and functional analyses using VIGS and CRISPR-Cas9 confirmed the phenotype is caused by the mutation of a HD-ZIP I transcription factor, SlHDZ38. Furthermore, an RNA-seq analysis suggest that SlHDZ38 has a key role in regulating both trichome-specific transcription factors and volatile terpenes specialized metabolism.

Chapter 5 discusses how all the findings described in the thesis expand and refine our understanding of the network of transcription factors regulating tomato type VI trichome development and specialized metabolism.

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