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REVIEW PAPER

The roles of trichome development genes in stress resistance

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Abstract

Trichomes are important epidermal structures that cover the surfaces of most terrestrial plants. Plants face various stresses due to their immobile nature, and trichomes play important roles in defense against environmental stressors including herbivores, strong light with high radiation, and ultraviolet light. 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. In the current review, we classify trichome development genes based on whether they are involved in trichome initiation, differentiation, and branching. Most of these genes encode transcription factors that positively or negatively regulate trichome development. Given that trichomes play key roles in plant stress responses, we explore whether trichome development-related genes also participate in other biological processes or responses, such as biotic and abiotic stress responses. Possible interactions of signaling pathways that function in trichome development and stress resistance were discussed. Elucidating the trichome development mechanism in model plants should shed light on the development of similar structures in other species and uncover key genes involved in these processes. Further characterizing these genes should facilitate the use of genetic engineering to improve stress resistance in crops.

Keywords Development · Genes · Plants · Stress resistance · Trichomes

Introduction

Terrestrial plants are rooted in the soil, meaning they must adapt to their complex, changeable environments throughout growth and development. Epidermal hair-like structures evolved during the transition of plants from the ocean to the land (Chopra et al. 2019). These structures, known as trichomes when found on the aerial organs of plants and root hairs when found underground (Doroshkov et al. 2019), are extensions of the epidermis (Fambrini and Pugliesi 2019) that play important roles in the interactions between plants and the environment (Zhou et al. 2018). The definition of trichome refers to a epidermal and hairy outgrowth on a plant's surface, as a prickle, is presented (Huchelmann et al. 2017).

Trichomes are present on the leaves, stems, inflorescence stems, and flowers of most terrestrial plants (Chopra et al. 2019), functioning as the first line of defense against physical damage from biotic stress (such as insect herbivores, pathogenic fungi, and bacteria) and abiotic stress (e.g., reflecting light to protect plants from strong light) (Kariyat et al. 2018). Their size ranges from microns to centimeters: cotton (*Gossypium herbaceum* L.) trichomes can reach up to 20 cm in length, while *Arabidopsis thaliana* trichomes are generally only a few millimeters long when mature (Wang et al. 2019b; Guan et al. 2008). Some trichomes, such as prickles in tomato (*Solanum lycopersicum*), have adjunct structures that function as biochemical factories to biosynthesize a diverse array of specialized metabolites (Kang et al. 2014). For example, trichomes of *Artemisia annua* produce artemisinin, a sesquiterpenoid used as a well-known antimalarial drug (Singh et al. 2016). The raw materials used by the natural fiber and textile industry primarily come from the trichomatous fibers of the cotton seed coat (Rinehart et al. 1996). Polysaccharides, proteins, polyphenols, and terpenoids are synthesized in the trichomes of many plants, such as *A. annua*, hops, and mint, and can be used to manufacture drugs, fragrances, and natural pesticides (Lange and

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Turner 2013). For example, the trichome of *A. annua* can produce artemisinin, which is a sesquiterpene antimalarial drug (Singh et al. 2016); the accumulation of toxic compounds (primin, chlorogenic acid and rutin) in the trichome can improve the resistance to insects, microbes and herbivores (Wagner et al. 2004).

Trichomes can be classified in many different ways, including by whether they secrete substances (such as acids and carbohydrates), their number of cells or branches, their shape, or their size. The first two categories are the most commonly used, particularly because the number of branches is related to the secretory functions of trichomes. There are evidences that species with more trichome branches seem generate fewer secretions. For example, the Arabidopsis trichomes, with 3–4 branches, do not secrete substances, but tobacco (*Nicotiana tabacum*) trichomes, with no branches, produce abundant secretions (Cui et al. 2011). Figure 1 shows the general structures of secretory and non-secretory trichomes, with the former displaying secretory pores and the latter possessing branches. Typical secretory unbranched trichomes, like those observed in tobacco, are shown in Fig. 1a. Non-secretory trichomes, such as those in Arabidopsis, are shown in Fig. 1b; these trichomes function in defense against biotic and abiotic stresses (Yan et al. 2012).

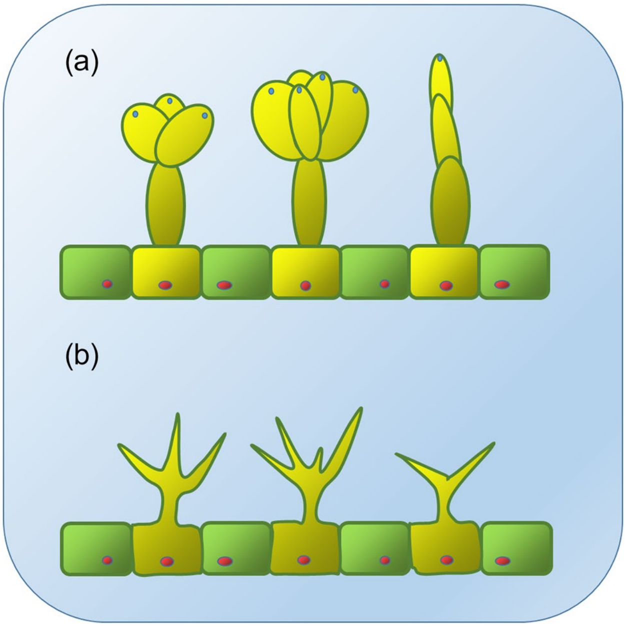

Fig. 1 Structures of glandular (secretory) and non-glandular (non-secretory) trichomes. **a** Glandular trichomes are usually composed of multiple cells of different shapes and have secretory pores, such as those in *Nicotiana tabacum*; the blue circles represent secretory pores. **b** Non-glandular trichomes are generally single-cell structures, with one to five branches, such as those in *Arabidopsis*. (Color figure online)

Trichomes can also be classified as single-celled or multicellular, although they are usually instead grouped based on whether they are glandular or non-glandular, which have different functions in plant defense. Non-glandular trichomes are mainly used as mechanical barriers by plants to restrict the movement of herbivores and avoid damage by feeding (Murungi et al. 2016). Unlike non-glandular trichomes, glandular trichomes secrete phytochemicals that induce the expression of certain defense genes or secretions that directly target and disperse herbivores (Glas et al. 2012),such as *EXPRESSION OF TERPENOIDS 1* (*SLEOT1*), which functions in terpene biosynthesis in tomato trichomes (Spyropoulou et al. 2014; Schuurink and Tissier 2020).

The number of trichomes and their secretion ability affect plant resistance to biotic stress. Trichomes are also involved in plant resistance to some abiotic stresses; for example, plants often produce more trichomes when grown under high salt or drought-stress conditions (Yuan et al. 2019). Trichomes can also reflect light to protect plants against damage by ultraviolet radiation (Escobar-Bravo et al. 2019). The enhanced expression of trichome development-related genes also contributes to plant resistance to some stresses (Yuan et al. 2019). These facts prompted us to ask in this review: Is there a relationship between trichome development genes and stress resistance? As trichome development is well characterized in the model plant Arabidopsis (Chang et al. 2019), we will primarily focus on whether the genes involved in trichome differentiation in this plant are also involved in stress resistance. The insights gained on this topic could aid efforts to improve stress resistance in a wide variety of crops, economic plant and forestry species.

Proposed model for trichome development of Arabidopsis

Trichome differentiation in Arabidopsis is triggered in individual cells which are considered as protodermal cells. Figure 2 shows a model of the roles of the genes (most of which encode transcription factors) known to participate in trichome development in Arabidopsis (Chang et al. 2019; Doroshkov et al. 2019), including the initiation, differentiation, multidimensional cell growth, and branching of these epidermal structures. Transcription factors with both negative and positive effects on their target genes drive these processes (Wang et al. 2019a). Here, we provide a brief summary of the genes known to be involved in trichome development.

Trichome initiation

As shown in Fig. 2a, the positive regulators GLABRA1 (GL1), GLABRA3 (GL3), ENHANCER OF GLABRA3

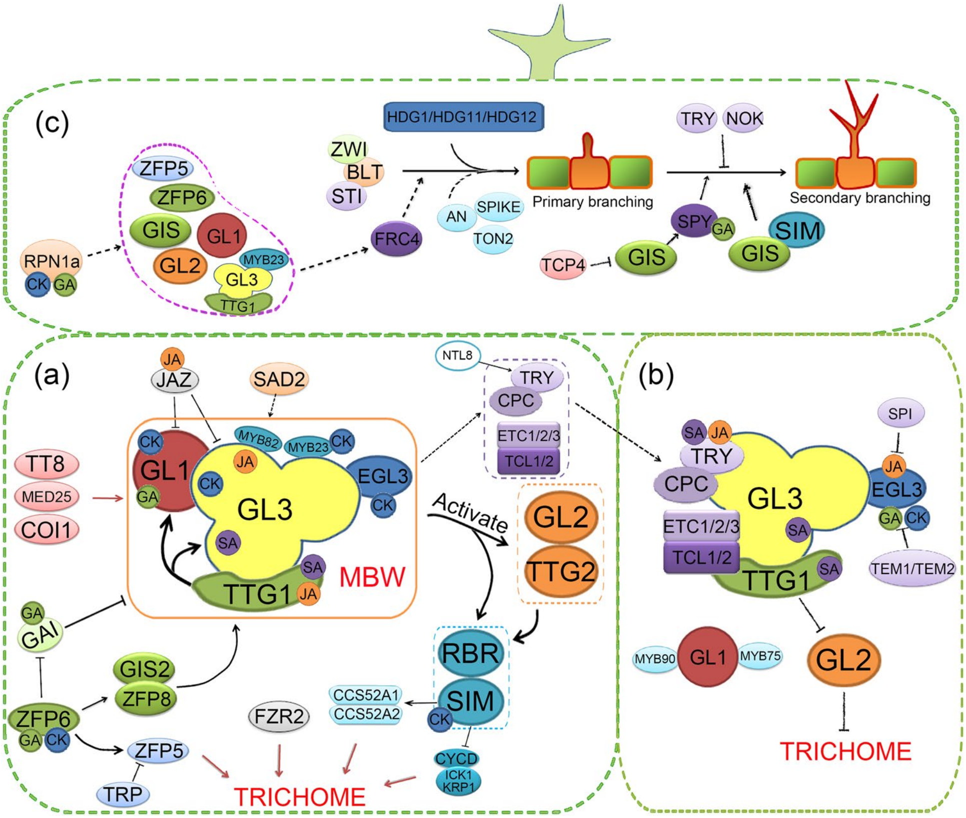

Fig. 2 Proposed model of trichome development. **a** Trichome initiation and differentiation. *GL1, GL3, EGL3*, and *TTG1* form a MYB-BHLH-WDR (MBW) activation complex to activate the expression of *GL2*/*TTG2* andRBR/SIM to promote the formation of trichomes. TT8/MED25/COL1, SAD2 and GIS2/ZFP8 play a positive role in the upstream of MBW complex, while JAZ and GAI negatively regulated the formation of MBW complex. After initiation, the down regulated genes *CCS52A1*/*CCS52A2*, *FZR2*, *ZFP5*, and *ICK1*/*KRP1* cooperatively control the differentiation of trichome. **b** Repression of trichome formation. Simultaneously, TRY/CPC/ETC1/ETC2/ETC3/TCL1/TCL2 are induced and rapidly move to the adjacent cells, which can competitively combine with GL3 and replace GL1 to inhibit trichome initiation. **c** Arabidopsis trichomes undergo two consecutive branching events. Primary branching of trichomes is regulated by *ZWI, STI*, and *BLT* and secondary branching is promoted by *SPY* and *GIS*/*SIM.* The plant hormones cytokinins (CK) in blue circle, gibberellins (GA) in green, salicylic acid (SA) in purple and jasmonic acid (JA) in orange play positive roles in regulating trichome development. → indicates promoting and ——| means inhibiting. Dotted lines represent no clear evidence of interaction

(EGL3), and TRANSPARENT TESTA GLABRA1 (TTG1) form a MYB-bHLH-WDR (MBW) activator complex to activate the expression of *GL2*/*TTG2* and RBR/SIM, thereby promoting trichome initiation (Yang et al. 2013; Morohashi et al. 2007; Morohashi and Grotewold 2009; Payne et al. 2000; Zhang et al. 2003). In general, TTG1 acts upstream of *GL3* and *GL1* to activate their expression (Payne et al. 2000). *SENSITIVE TO ABA AND DROUGHT2* (*SAD2*) encodes an important beta-domain protein that regulates trichome development in the same manner as *GL1*, *GL2*, and *GL3* (Zheng et al. 2020). Competitive combination with GL3 occurred between MYB transcription factors CAPRICE (CPC), TRIPTYCHON (TRY), and GL1 to regulate trichome initiation (Schnittger et al. 1999; Wada et al. 1997; Kirik et al. 2001). The transcription factors TRY and CPC are negative regulators of trichome initiation that compete with GL1 for binding to the bHLH protein GL3 or ENHANCER OF GLABRA3 (EGL3), thereby altering the MBW complex so that cells cannot form trichomes (Fig. 2b).

Specifically, trichomes are derived from rapidly dividing protoepidermal cells at the bases of new leaves. After four rounds of endoreduplication, the trichomes mature and form two to four branches, depending on the plant species (Melaragno et al. 1993; Larkin et al. 2003). The induction of cell divisions during the early steps of glandular trichome development requires not only transcription factors, but also cell cycle regulators. Various proteins regulate the cell cycle to induce trichome initiation, such as SIAMESE (SIM) and RETINOBLASTOMA-RELATED (RBR), which regulate the expression of the cyclin-dependent kinase genes *CCS52A1* and *CCS52A2* (Kasili et al. 2010; Desvoyes et al. 2014; Sun et al. 2013). SIM, a repressor of mitosis during the internal replicating cell cycle, is required to coordinate cell division and differentiation during Arabidopsis trichome development (Walker et al. 2000). Overexpressing *CYCD* in trichomes led to the production of multicellular trichomes in wild-type plants. Conversely, the multicellular trichome phenotype of the *sim* mutant was rescued when the cyclin-dependent kinase (*CDK*) inhibitor gene *ICK1/KRP1*, which interacts with *CYCD*, was exogenously expressed in trichomes (Wang et al. 2020).

SIM and *RBR* expression is positively regulated by GL2 and TTG2 (Khosla et al. 2014) but negatively regulated by TRY, CPC, ENHANCER OF TRY AND CPC1 (ETC1), ETC2, ETC3, TRICHOMELESS1 (TCL1), and TCL2 (Payne et al. 2000; Chen and Schmidt 2015; Wang et al. 2007; Tian et al. 2017; Gan et al. 2011). NTM1-LIKE8 (NTL8) negatively regulates trichome formation in Arabidopsis by directly activating the expression of *TRY* (Tian et al. 2017). MYB82 also interacts with *GL3* at one of its two exons, thereby regulating trichome development (Liang et al. 2014). MYB75, MYB90, and GL1 interact to inhibit trichome initiation (Teng et al. 2005; Mondal et al. 2018). TRICHOME-RELATED PROTEIN (TRP) is only produced in trichomes, where it binds to ZINC FINGER PROTEIN 5 (ZFP5) and inhibits its binding to the *ZFP8* promoter region (Kim et al. 2018; Zhou et al. 2011). Thus, TRP and ZFP5 play opposite roles in regulating trichome initiation. FIZZY-RELATED2 (FZR2) controls the induction of early endoreduplication, as *FZR2* is necessary and sufficient for specific rounds of endoreduplication in Arabidopsis. The loss-of-function *fzr2* mutants show reduced numbers of endoreduplication cycles in the trichome and reduced trichome branching (Larson-Rabin et al. 2009).

The homologous genes in other species also showed the similar functions. The conserved AP2 domain protein OsGL6 promotes leaf trichome initiation in rice (*Oryza sativa* L.) (Xie et al. 2020). Conversely, OCL4 might inhibit trichome development. Expressing the maize gene *OCL4* (encoding an HD-ZIP IV transcription factor involved in trichome differentiation) under the control of the *GL2* promoter did not complement the abnormal trichome expansion of the Arabidopsis *gl2-1* mutant but instead aggravated its phenotype (Vernoud et al. 2009). Overexpressing the cotton (*Gossypium arboreum*) annexin gene *AnnGh3* in Arabidopsis resulted in significant increases in trichome density and leaf length, suggesting that *AnnGh3* is involved in fiber cell initiation and elongation in cotton (Li et al. 2013). Rice contains two R3MYB transcription factor genes: *Oryza sativa TRICHOMELESS1* (*OsTCL1*) and *OsTCL2*. Expressing *OsTCL1* in Arabidopsis inhibited trichome formation and promoted root hair formation, and OsTCL1 interacted with GL3 in Arabidopsis protoplasts (Zheng et al. 2016).

Hormonal regulation of trichome differentiation

Following trichome initiation, many hormones and genes influence the differentiation of these structures (Fig. 2a), and different hormones interact with each other during this process. Salicylic acid (SA) regulates the transcription of *GL3*, *TTG1*, and *TRY* (Traw and Bergelson 2003), while jasmonate (JA) regulates the formation of trichomes by promoting the degradation of ZIM domain JAZ proteins to prevent their interaction with *GL1* and *EGL3/GL3* (Wen et al. 2018; Guo et al. 2018). SPI inhibits JA biosynthesis (Hohl et al. 2017), whereas the transcription factors TRANSPARENT TESTA8 (TT8), MED25, and CORONATINE INSENSITIVE 1 (COI1) promote this process (Wen et al. 2018; Fornero et al. 2017), and JA promotes the transcription of *GL3*, *TTG1*, and *TRY* (Wen et al. 2018; Qin et al. 2011) (Tian et al. 2016). GA directly promotes trichome development by increasing the transcription of *GL1* (Tian et al. 2016). DELLA proteins inhibit the GA signal transduction pathway, which is encoded by five genes: *GIBBERELLIC ACID INSENSITIVE* (*GAI*), *REPRESSOR OF ga1-3* (*RGA*), and three *RGA-LIKE* genes (*RGL1*, *RGL2*, and *RGL3*). DELLA proteins interact with the basic components of the WD-repeat/BHLH/MYB complex to modulate the synergistic effects of GA and JA signaling on trichome development (Fuentes et al. 2012). Cytokinin (CK) stimulates the expression of *GL1*, *GL3*, *MYB23*, *EGL3*, and *SIM* (Gan et al. 2007). ZFP6 integrates GA and CK signaling and acts as an upstream activator of *ZFP5* expression (Khosla et al. 2014), which in turn upregulates the expression of *GLABROUS INFLORESCENCE STEMS* (*GIS*), *GIS2*, and *ZFP8* (Fig. 2a) (An et al. 2012; Gan et al. 2007). In addition, GIS2 and ZFP8 can increase the transcription of *GL1* and *GL3*, meaning that *GIS* acts upstream of the MBW complex and has the opposite effect of the repressor gene *GAI* (An et al. 2012; Gan et al. 2006; Zhang et al. 2018). Finally, TEMPRANILLO1 (TEM1) and TEM2 negatively regulate trichome formation by affecting the biosynthesis of GA and CK (Fig. 2b) (Gan et al. 2006).

Trichome branching

After their differentiation, some trichomes undergo two branching events (Fig. 2c): primary branching and secondary branching. *ZWICHEL* (*ZWI*) and *STICHEL* (*STI*) are thought to promote the primary branching of trichomes by directly interacting with *BRANCHLESS TRICHOME* (*BLT*), an important protein linking cell shape and endoreplication (Kasili et al. 2011; Reddy et al. 2004). *ANGUSTIFOLIA* (*AN*), *FASS/TONNEAU2* (*TON2*), and *SPIKE* participate in trichome branching by regulating microtubule arrangement in plant tissue (Kim et al. 2002). Homeodomain glabrous (*HDG*) transcription factors including *HOMEODOMAIN GLABROUS1 (HDG1), HDG11*, and *HDG12* function in trichome branching by promoting cell differentiation (Horstman et al. 2015). The 26 S proteasome subunit RPN1a also inhibits trichome branching in Arabidopsis by promoting the transcription of *ZFP6*, *ZFP5*, *GIS*, *GL1*, *GL2*, *GL3*, *TTG1*, and *MYB23*, leading to increased *FRC4* expression in trichomes (Yu et al. 2015). RPN1a might also function in the GA and CK signaling pathways to influence trichome development (Zhu 2016).

Many proteins play positive or negative roles in regulating secondary branching in trichomes. *TRY* and *NOK* encode negative regulators of this process, as the loss of function of these genes leads to the generation of additional branch points (Lescot et al. 2002). GIS regulates trichome branching by regulating two different branching pathways in Arabidopsis: the negative regulatory factors that function upstream and downstream of *SPINDLY* (*SPY*) in the GA signaling pathway (Lescot et al. 2002). GIS also play an indirect role in regulating hairy cell division by interacting with SIM (Qin et al. 2011; Cui et al. 2014). The miR319-regulated PROLIFERATING CELL FACTOR4 (TCP4) protein suppresses trichome branching by directly activating *GIS* transcription in Arabidopsis leaves (Vadde et al. 2018).

Trichome development genes that participate in stress resistance

Unfavorable environmental conditions, including biotic and abiotic stress, inhibit plant growth, development, and reproduction (Gong et al. 2020). Biotic stress responses in plants are induced by viruses and microorganisms, as well as the feeding of insects and other herbivores. By contrast, abiotic stresses include drought, salt, cold, heat, heavy metals, and ultraviolet rays (Shao et al. 2021). Here, we focus on the roles of trichome development genes in stress resistance.

Biotic stress resistance

Non-glandular structures can block the movement of herbivorous arthropods on the plant surface or prevent the mouth parts of insects from reaching the plant surface, for example, the tips of the trichomes hinder the movement of insect (Glas et al. 2012). Some glandular structures produce acyl sugars or polyphenols, which trap the insect in their secretions, where it ingests toxins or suffocates to death (Karamanoli et al. 2012). Trichomes can hinder the movement and biting of insects (Sato et al. 2019), but they can also detect the physical signal of insect movement and act as a mechanoreceptor to induce a series of internal reactions such as JA and SA production (Glas et al. 2012; Cardoso 2008). In Arabidopsis, trichomes detect insect movement as the buckling of the cell walls from the base to the branch tips, which induces cytoplasmic calcium oscillations and changes in extracellular pH that are transferred to neighboring cells (Reddy et al. 2004). In general, wild wheat has stronger stress defense abilities than the domesticated wheat (Tanno and Willcox 2006), while there are also evidences that some domesticated varieties may have stronger defense mechanisms against insects than wild wheat. Domesticated wheat employs two major mechanisms for insect defense: biosynthesis of the deterrent compounds benzoxazinoids, and trichome formation to provide a physical barrier against insect attack (Batyrshina et al. 2020).

The trichome-initiation gene *GL1* plays a key role in the physical defense against herbivores, particularly leaf-gnawing insects. A negative correlation was detected between the total abundance of leaf-eating insects and the density of trichomes. The loss of function of *GL1* significantly reduced plant resistance to herbivorous insects (Sato et al. 2019). In addition to this genetic regulator, JA, a key hormone involved in trichome differentiation, is essential for defense against biotic stress (Kennedy 2003). In general, injury and/or herbivore infestation activates the octadecanoic acid pathway, leading to increased levels of JA, which trigger the expression of defense genes (such as genes encoding protease inhibitors) and the accumulation of secondary metabolites involved in plant defense (such as terpenes) (Wei et al. 2019). In addition to regulating the defense response induced by herbivores, the production of many metabolites in trichomes is also subject to strict transcriptional control downstream of hormonal regulation, allowing for the temporary regulation of plant volatile production (Huchelmann et al. 2017; Glas et al. 2012).

UV and ozone resistance

UV-B increases the density of leaf trichomes to reflect excessive light and reduce transpiration (Escobar-Bravo et al. 2019), at least in part by inducing the expression of the trichome-initiation gene *GL3* (Morohashi and Grotewold 2009). Mutants with more trichomes than the wild type are more resistant to UV-B, while mutants with fewer trichomes are more sensitive to UV-B, indicating that trichomes play a key role in protecting plants against UV-B irradiation (Yan et al. 2012). Some plants accumulate UV-absorbing compounds in their trichomes, such as flavonols, which can protect the underlying photosynthetic tissue from damaging amounts of UV-A and UV-B irradiation (Agati and Tattini 2010; Agati et al. 2012).

In addition, plants with lower glandular trichomes densities are more sensitive to ozone stress and more susceptible to ozone destruction than the wild type (Li et al. 2018). Glandular trichomes on the leaf surface are major factors in reducing ozone toxicity by acting as chemical barriers to neutralize ozone before it enters the leaf. Therefore, leaf trichomes might be an important driving force for the spread of species in polluted environments (Lihavainen et al. 2017).

Salt and drought resistance

Plants have evolved several strategies to respond to environmental changes (Zhu 2016). The drought and salt-stress responses share some common signal transduction mechanisms; for example, in addition to ion toxicity, salt stress causes hyperosmotic stress, which is also observed in drought-stressed plants (Gong et al. 2020). Salt stress can also cause some secondary injuries, such as oxidative stress, which can destroy cellular components and affect the metabolic functions of cells.

Many trichome development genes are responsive salt stress (Li et al. 2018). The Arabidopsis *SPI* gene encodes a WD40/BEACH domain protein involved in trichome development, the deletion of which results in the formation of distorted trichomes. SPI also participates in salt resistance by interacting with the P-body core component DECAPPING PROTEIN1 (DCP1) to maintain membrane integrity (Qin et al. 2011). The plant-specific homeodomain leucine zipper (HD-Zip) gene family plays a vital role in trichome development and abiotic stress responses (Khosla et al. 2014; Zhang et al. 2019; Chen et al. 2016). In Arabidopsis, four HD-ZIP-IV genes—*GL2*, *MERISTEM LAYER1* (*ML1*), *PROTODERMAL FACTOR2* (*PDF2*), and *ANTHOCYANINLESS2* (ANL2) are involved in trichome development (Zhang et al. 2016, 2019), the determination of floral organ characteristics (Vernoud et al. 2009; Kamata et al. 2013), epidermal cell proliferation (Javelle et al. 2011), and root development and anthocyanin accumulation (Elhiti et al. 2009). HDG11 and HDG12 are closely related feature-rich HD-ZIP-IVs that regulate trichome branching (Horstman et al. 2015). Most HD-ZIP-IV genes are induced by heat, cold, salt, drought, and the exogenous application of the plant hormones GA, 6-benzylaminopurine, and SA, but are inhibited by abscisic acid (ABA) in *N. tabacum* (Elhiti et al. 2009) (Chew et al. 2013). Salt stress alters the CG methylation level of *GL2*, leading to the production of more root hairs and fewer trichomes than the control (Gan et al. 2006).

The MYB family, one of the largest transcription factor families in plants, includes several genes known to participate in trichome development and abiotic stress responses in Arabidopsis (Stracke et al. 2001; Li et al. 2019). Most MYB proteins belong to the R2R3-MYB subfamily (Kranz et al. 1998; Kirik et al. 2001; Stracke et al. 2001; Chen and Schmidt 2015), many of which are involved in regulating abiotic stress responses; for example, MYC2 and MYB2 actively regulate the expression of ABA-dependent genes under drought and salt stress (Abe et al. 2003). The trichome-initiation gene *GL1* is also a MYB family member. The loss of function of *GL1* affects trichome development, but the phenotype of the *gl1* mutant was restored by overexpressing *MYB82* (Liang et al. 2014), which interacts with *GL3*. *CPC* and related genes (such as *CPC-LIKE MYB 3* [*CPL3*]) encode MYBs, many of which regulate epidermal cell differentiation (Wada et al. 1997). *TTG2* functions redundantly with *GL2* in regulating trichome growth. *TTG2* encodes a WRKY transcription factor that acts downstream of *TTG1* and *GL1*. Therefore, *TTG2* and *GL2* can complement each other's activity to regulate the development of downstream targets and trichomes when plants are confronted by sudden environmental changes or foreign invasion (Johnson et al. 2002). OsSPL10, an SBP-box gene, negatively regulates salt tolerance but positively regulates trichome formation in rice (Lan et al. 2019).

The ABA signaling pathway is a core pathway in the drought and salt-stress responses, in addition to playing a role in JA signaling and regulating the ethylene response pathway (Kazan 2015). The discovery of the ABA pathway and the associated receptors was one of the most important advances in the study of stress signals in the past decades (Fujii and Zhu 2009). The trichome development genes *SPI*, *GAI*, *RGA*, *RGL1*, and *RGL2* respond to ABA, linking trichome patterning to the prevailing drought and salt conditions (Shi et al. 2017).

There is substantial evidence that Arabidopsis plants with more trichomes have higher salt tolerance than other plants (Yuan et al. 2019; Beyrne et al. 2019; Zhou et al. 2018). The mechanisms for the initiation of trichomes and root hair development share the same genes but with the opposite functions, such as *TTG1*, *TRY*, and *CPC* (Kirik et al. 2004; Wang et al. 2010; Ishida et al. 2008); thus, some factors that play positive roles in trichome formation may inhibit root hair development. Fewer root hairs are always observed in mutants with higher numbers of trichomes (Yuan et al. 2019), perhaps due to the decreased accumulation of Na^+ under salt-stress conditions.

Conclusions and perspectives

Trichomes are epidermal hairs that cover the aerial parts of most terrestrial plants. The formation of trichomes requires the cooperation of a series of genes (Fig. 2), which regulate trichome initiation, differentiation, branching, and morphology (Chang et al. 2019). Many of these genes are also involved in plant responses to biotic and abiotic stress. Table 1 provides a summary of the genes known to participate in both trichome development and stress responses.

Of course, some plants do not produce trichomes and instead have a smooth, hairless epidermis. These plants have all evolved alternative structures in the epidermis, such as salt glands and salt bladders, which are thought to employ a similar mechanism to trichomes (Yuan et al. 2016). Salt

Table 1 Trichome development genes related to stress resistance

Gene	Role in trichome development	Role in stress resistance	References	Species
GL1	Initiation	Jasmonic acid-mediated signaling pathway	Morohashi and Grotewold (2009)	*Arabidopsis thaliana*
GL3	Initiation	Jasmonic acid-mediated signaling pathway	Yoshida et al. (2009)	*Arabidopsis thaliana*
MED25	Initiation	Jasmonic acid-mediated signaling pathway	Fornero et al. (2017)	*Arabidopsis thaliana*
MYB75	Initiation	Jasmonic acid-mediated signaling pathway, removal of superoxide radicals	Teng et al. (2005)	*Arabidopsis thaliana*
MYB90	Initiation	Response to salt stress	Mondal et al. (2018)	*Arabidopsis thaliana*
NTL8	Initiation	Response to salt stress, negative regulation of gibberellin-mediated signaling pathway	Tian et al. (2017)	*Arabidopsis thaliana*
OsSPL10	Initiation	Response to salt stress	Lan et al. (2019)	*Oryza sativa L.*
COI1	Differentiation	Jasmonic acid-mediated signaling pathway	Bomer et al. (2018)	*Arabidopsis thaliana*
GAI	Differentiation	Response to salt stress, abscisic acid, ethylene, jasmonic acid-mediated signaling pathway, negative regulation of gibberellin-mediated signaling pathway	Fuentes et al. (2012), Wild et al. (2012), Qi et al. (2014)	*Arabidopsis thaliana*
GIS	Differentiation	Gibberellin-mediated signaling pathway	Gan et al. (2006), An et al. (2012), Sun et al. (2013)	*Arabidopsis thaliana*
GIS2	Differentiation	Gibberellin-mediated signaling pathway, response to cytokinin	Sun et al. (2013), Gan et al. (2007)	*Arabidopsis thaliana*
RGA	Differentiation	Response to salt stress, abscisic acid, ethylene, jasmonic acid-mediated signaling pathway, negative regulation of epidermal hair morphology, hypertonic salinity response, gibberellin-mediated signaling pathway	Silverstone et al. (1998, 2001), Wild et al. (2012)	*Arabidopsis thaliana*
RGL1	Differentiation	Response to salt stress, abscisic acid, ethylene, jasmonic acid-mediated signaling pathway, negative regulation of epidermal hair morphology, hypertonic salinity response, gibberellin-mediated signaling pathway	Silverstone et al. (1998, 2001), Wild et al. (2012)	*Arabidopsis thaliana*
RGL2	Differentiation	Response to salt stress, abscisic acid, ethylene, jasmonic acid-mediated signaling pathway, negative regulation of epidermal hair morphology, hypertonic salinity response, gibberellin-mediated signaling pathway	Wild et al. (2012), Silverstone et al. (2001), Yang et al. (2020)	*Arabidopsis thaliana*
SPI	Differentiation	Response to salt stress, abscisic acid	Qin et al. (2011), Cui et al. (2014)	*Arabidopsis thaliana*
TT8	Differentiation	Jasmonic acid-mediated signaling pathway	Wen et al. (2018)	*Arabidopsis thaliana*
ZFP5	Differentiation	Gibberellin-mediated signaling pathway, cytokinin-activated signaling pathway	Kim et al. (2018)	*Arabidopsis thaliana*
ZFP6	Differentiation	Gibberellin-mediated signaling pathway, cytokinin-activated signaling pathway	Zhou et al. (2013)	*Arabidopsis thaliana*

glands and trichomes share many similarities; for example, they are the first structures to differentiate during epidermis formation and are therefore detected earlier than stomata. During salt gland development in the halophyte *Limonium bicolor*, many genes typically associated with the initiation of trichome development are expressed, such as *GL1*, *TTG*, *GL3*, *TRY*, and *CPC* (Leng et al. 2018). The heterologous overexpression of *L. bicolor* genes related to salt gland development significantly complemented the phenotype of an Arabidopsis mutant lacking trichomes and improved salt resistance in the transgenic lines (Yuan et al. 2019). Given that many trichome differentiation genes also participate in stress resistance, these genes might also be related to the differentiation of other epidermal structures. Therefore, the current review provides candidate resistance genes that could be used to study the relationship between the origin and evolution of trichomes and salt glands.

We also noticed that trichome-initiation genes such as *TTG1*, *GL3*, and *GL2* always repress root hair determination, (Yang et al. 2013; Morohashi et al. 2007; Morohashi and Grotewold 2009; Payne et al. 2000; Zhang et al. 2003), as mutants of these genes are deficient in trichome differentiation and show enhanced root hair initiation. Therefore, a regulatory mechanism must exist that determines the different functions of these genes in different developmental directions depending on the plant region, such as the aerial or underground parts of the plant. How the same gene participates in opposite developmental processes in different parts of the same plant is another interesting question to address in the future.

Little is known about origin and evolution of plant trichomes, except for the structures and functions of the underlying gene regulatory networks described by Doroshkov et al. (2019). It is still challenging to describe how the roles of trichome-related genes have evolved over time. Trichomes do not exist in all plants; however, current evidence indicates that homologs of trichome development-related genes function in similar epidermal structures. These homologs share the same conserved, function-specific domains that enable the induction of different structures and enhance stress resistance. Further analysis of the roles of genes involved in both trichome development and stress resistance may therefore shed light on the differentiation of similar structures. The mechanisms by which trichome development genes participate in stress-response pathways (such as the salt-stress response) are still largely unknown; thus, more research is needed to study the roles of key genes in stress-response signaling pathways and in regulating the development of other epidermal structures.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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