

Trichome, a Functional Diversity Phenotype in Plant

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Abstract

Trichomes play a very important role in the process of evolution for plant which are epidermal appendages covering the surface of plants. In this paper, some progress concerning the genes responsible for trichome formation is presented for monocots and dicotyledons plants. Meanwhile, the special structures and physiological functions of trichome are briefly introduced, such as reflectance, energy balance, ultraviolet protection, drought resistance, gas exchange, insect resistance and disease resistance. The review provides a theoretical basis for the further study of other trichome related traits in plants.

Keywords: Trichome; Functional diversity; Phenotype; Plant

Introduction

Trichomes, as a plant protective barrier against natural hazards such as herbivores, ultraviolet (UV) irradiation, pathogen attacks and excessive transpiration, play a key role in development of plants and occur widely in various plants. Trichomes may be unicellular or multicellular and are derived from aerial epidermal cells in leaves, stems and floral organs. They are classified as either glandular or non-glandular [1,2]: the former can contribute to the accumulation and secretion of some alkaloids to resist insects, such as nicotine and terpenoid alkaloids, and the latter can strengthen the role of resistance in abiotic stress by promoting normal plant growth, under condition of extreme high or low temperature, drought and UV irradiation [3,4]. The origination and spatial and temporal distribution of trichomes are well suited mechanisms for studying cell differentiation, fate choices and morphogenesis [5,6]. Over time, some previously unknown mechanisms have been elucidated (Figure 1).

Structure characteristics of trichomes

Trichomes are a model system for cell differentiation, cell cycle regulation, cell polarity and cell expansion, according to different distributions on leaves, and can be divided into three categories: large, small and glandular trichomes [8,9]. Large trichomes are commonly observed on the abaxial surface, above the vascular bundles and along the margins, small trichomes in stomatal Para cellular and glandular trichomes, which are regularly distributed wholly or partly in sub epidermal tissue of the leaf surface [10]. Trichomes are not obvious in the early developmental stage, and can be observed at three-leaf stage. The early stages of trichome morphogenesis can be divided into four stages: (1) the radial trichome precursor cells protrude from the blade surface, (2) the rod structure of trichomes appears and enlarges, (3) branch structure is formed, (4) the rod structure and branch further increase with the tips of branches being blunt. With further development of trichomes, the rod-shaped structure and branches continue to expand and the branch tip becomes sharp, and then forms mature trichomes with papilla on the leaf surface [11,12].

The distribution and morphology of trichomes are related to many factors that include geography. For example, the stems of tomato are covered with long trichomes, but trichomes are short and scarce in the upper parts of the stem [13]. Moreover, the density distribution of trichomes varies in different organs: and the density of trichomes on the back of the same blade was significantly higher than that of the back [14]. Brewer found that different types of leaves had different densities of trichomes, and in soybean leaves, the adaxial of the leaf had greater trichome density than the abaxial [15].

Genes related to the formation and development of trichomes

Increasing numbers of studies have focused on the localization and cloning of genes related to trichome growth, but molecular mechanisms remained unknown, especially in monocots plants such as *Oryza sativa*.

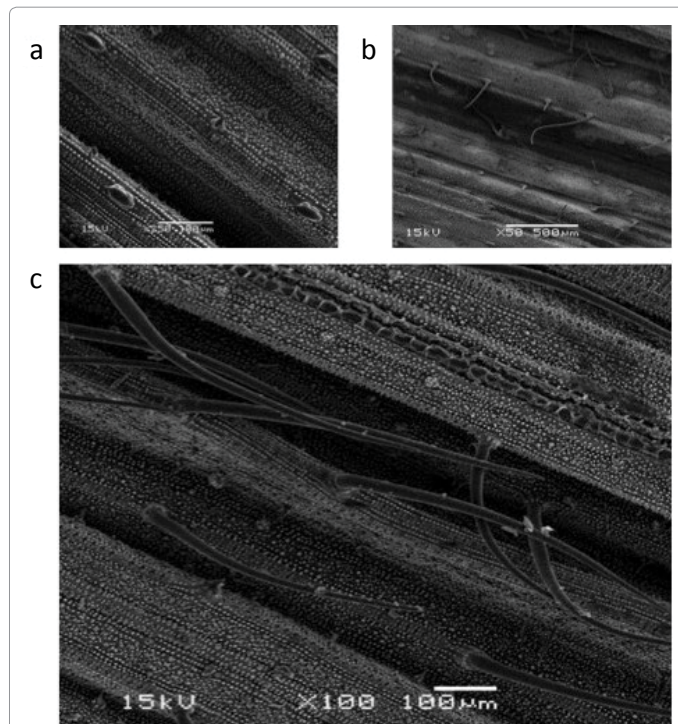


Figure 1: The development of trichome from rice (*Oryza sativa* L.) [7]; a) Trichome morphogenesis at early stages; b) Trichome morphogenesis at middle stages; c) Trichome morphogenesis at mature stages.

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Gene (Chr.)	Function	Species	References
<i>AtGL1</i> (Chr.3)	A myb-related gene required for leaf trichome differentiation	Arabidopsis	[20]
<i>AtGL2</i> (Chr.1)	HD-ZIP IV family of homeobox-leucine zipper protein with lipid binding START domain-containing	Arabidopsis	[11]
<i>AtGL3</i> (Chr.5)	basic helix-loop-helix (bHLH) DNA-binding superfamily protein	Arabidopsis	[18]
<i>AtTTG1</i> (Chr.5)	Transducin/WD40 repeat-like superfamily protein	Arabidopsis	[19]
<i>AtTRY</i> (Chr.5)	Homeodomain-like superfamily protein	Arabidopsis	[24]
<i>AtCPC</i> (Chr.2)	Homeodomain-like superfamily protein	Arabidopsis	[25]
<i>AtTCL1</i> (Chr.1)	Homeodomain-like superfamily protein	Arabidopsis	[26]
<i>AtTCL2</i> (Chr.2)	Homeodomain-like superfamily protein	Arabidopsis	[27]
<i>AtETC1</i> (Chr.1)	Homeodomain-like superfamily protein	Arabidopsis	[28]
<i>AtETC2</i> (Chr.2)	Homeodomain-like superfamily protein	Arabidopsis	[29]
<i>OsGL1</i> (Chr.5)	Homeodomain protein containing the WOX motif	<i>Oryza sativa</i>	[30]
<i>OsGL6</i> (Chr.6)	Unknown	<i>Oryza sativa</i>	[7]
<i>OsHLA/HLb</i> (Chr.9/11)	Complementary genes for long pubescence of leaves	<i>Oryza sativa</i>	[31]
<i>Wo</i> (Chr. 1)	Homeodomain protein containing a bZIP motif and a START domain	Tomato	[32]
<i>SICycB2</i> (Chr.2)	regulated by <i>Wo</i> , participates in trichome formation	Tomato	[32]
<i>GaHOX1</i> (Chr.7)	HD-Zip IV gene	Cotton	[33]
<i>GhMYBs</i>	regulates early fibre and trichome development	Cotton	[34]
<i>QLP1</i> (Chr.6)	reduced hairiness only in young leaves	Cotton	[35]
<i>QLP2</i> (Chr.25)	increased hairiness in mature leaves	Cotton	[35]
<i>RDL1</i> (Chr.4)	regulator of cotton fiber development	Cotton	[36]
<i>OCL4</i> (Chr.1)	The HD-ZIP IV transcription factor	Maize	[37]
<i>MHL1</i> (Chr.3)	Promote leaf blade macrohair initiation and responds to factors regulating leaf identity	Maize	[38]

Table 1: The cloned gene and their function from plants.

In *Arabidopsis thaliana*, a series of genes related to the formation and development of trichomes has been found (Table 1), including GIS, MYB23, GL3/EGL3, TTG1, GL1, GL2 and FRC4 [11,16-21]. As an important monocots plant and agricultural crop, the agronomic traits of *O. sativa* are crucially influenced by trichomes. Several relevant genes have been localized, for example, genes *OsGL1* and *OsGL6* located on chromosomes 5 and 6, respectively [7,22]. In addition, a number of orthologous genes have been identified, such as *TCL* in *Arabidopsis* to *OsTCL1* and *OsTCL2* in rice [23] (Table 1).

Regulation of trichome formation

The genetic network regulating trichome development has been extensively studied and well understood in the model species *Arabidopsis*, and shown to be regulated by a complex gene network (Figure 2) [39,40]. The genes that control trichome growth generally belong to the MYB transcription factor family, including the transcriptional activator of *GL2* [41], *GLABRA1* (*GL1*) [42], the WD40-repeat protein *TRANSPARENT TESTA GLABRA1* (*TTG1*) [1,43] and the basic helix-loop-helix (bHLH) transcription factors *GLABRA 3/ENHANCER OF GLABRA3* (*GL3/EGL3*) [44,45] which are key factors in the initiation of trichomes. The MYB transcription factor family is one of the largest transcription factor families in plant is based on variation in the number of N-terminal DNA-binding domain repeats (R) and has been divided into four subfamilies: 4R-MYB, 3R-MYB, R2R3-MYB and 1R-MYB containing four, three, two and one DNA-binding repeats, respectively [46]. It was proposed that *GL1*, *TTG1* and *GL3* or *EGL3* form a *GL1-GL3/EGL3-TTG1* activator complex to trigger the expression of *GL2*, leading to the promotion of trichome formation; interestingly, the same activator complex also induces expression of some single-repeat R3 MYB genes. Single-repeat R3 MYBs, in turn, move from a trichome precursor cell to its neighboring cells to block the formation of the activator complex by competing with *GL1* for binding to *GL3* or *EGL3*, thus limiting formation of the *GL1-GL3/EGL3-TTG1* activator complex and inhibiting trichome formation [47,48]. Studies showed

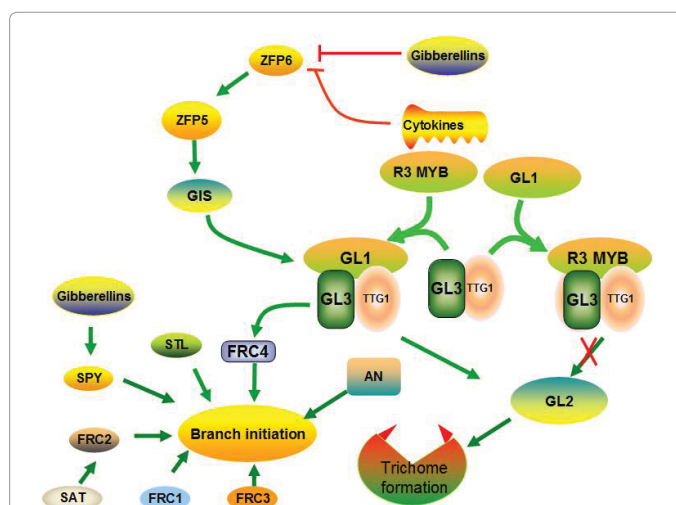


Figure 2: Signaling pathway for the regulation of the trichome in *Arabidopsis thaliana*.

The trichome were regulated by a complex gene network: 1) *GL1*, *GL3* or *EGL3* and *TTG1* form a *GL1-GL3/EGL3-TTG1* activator complex to trigger the expression of *GL2* leading to the promotion of trichome formation, 2) some single-repeat R3 MYB genes competing with *GL1* for binding to *GL3* or *EGL3* limiting the formation of the *GL1-GL3/EGL3-TTG1* activator complex and inhibiting trichome formation, 3) *GL3* can activate positively *FRC4* to affect trichome branching, in addition, there are also have many genes involved in trichomes branch regulation, including *FRC1-3*, *SPY*, *STL*, etc., 4) GA and CK may also involve in trichome formation by regulation the gene *ZFP6*, *ZFP5* and *GIS*, and regulate to form a *MBW* (MYB-bHLH-WD40) transcriptional activator complex to induce the expression of *GL2* and leading to the promotion of trichome formation

that *GL3* can activate *FRC4* to affect trichome branching [21,49]. *KAK* (*KAKTUS*) and *PYM* (*POLYCHOME*) are considered to be negative regulators of trichome branching. *PYM* and *KAK* act downstream of *SPY* (*SPINDLY*) to control the trichome branching pattern and number. *AN* (*ANGUSTIFOLIA*) promotes trichome branching, which

is negatively regulated by the MYB transcription factor NOK (NOEK); however, SPY is a gibberellins signaling repressor and the SPY deletion mutant has increased trichome branching [21].

Although there is evidence that trichome formation in other same dicotyledonous plants may be controlled by similar mechanisms, it may not be in dicotyledonous plants [23]. Zheng et al. [23] used the entire amino acid sequence of Arabidopsis R3 MYB transcription factor Trichomeless1 (TCL1) blasted in *O. sativa* and thus found OsTCL1 remained largely unchanged in transgenic rice plants, a gene can inhibit the formation of trichomes by interacting with GL3 in Arabidopsis protoplasts, which showed that rice may use different mechanisms to regulate trichome formation [50]. Until now, the only cloned gene in *O. sativa* to show control of trichome formation is OsGL1 [22], but the mechanism is not yet clear (Figure 2).

Apart from Arabidopsis and *O. sativa*, many genes that control the formation of trichome have been cloned in other plants, including HI2 and HI2Aesp, located on chromosome 4BL and 7BS in wheat, respectively [51]. A series of maize GLOSSY genes have been cloned and were shown to affect the morphology and trichome growth and cuticular wax biosynthesis [52,53]. Overexpression of the gene MIXTA led to the growth of a large number of trichomes on cotyledons, leaves and stems in tobacco, and another gene CotMYBA may cause the growth of *Nicotiana tabacum* leaf [54]. The gene that encodes the HD-Zip protein named Wo, which can interact with cell cycle gene B2, plays an important role in trichome formation and embryo development in potato [55].

Ecophysiology of leaf trichomes

In recent decades, many studies have demonstrated that trichomes have an extensive role in plant–environment interactions [56–58]. The best known is as light reflectors that reduce photo-inhibition and UV-B related damage to leaf photochemistry [57,59]. Dense trichomes can modulate leaf heat balance and photon interception, and consequently affect gas exchange traits [57,60,61]. Trichomes can protect against damaging UV radiation and modulate water relations on leaf surfaces and in the mesophyll [62]. In addition, plants with trichomes also have characteristics of insect and disease resistance [63,64].

Light reflectors and energy balance

Studies have shown that trichomes can be reflectors of broad-spectrum radiation, and play a physiologically significant role in modulating the plant energy balance [57,65,66]. When leaves are exposed in environments, this can regulate heat balance via transpiration cooling, which requires an adequate water supply or through reduced leaf absorption [66]. The reflectivity of the leaf surface changes with the seasons in some plants with a thinner leaf blade, trichomes can absorb 80% of the incident radiation in winter, so that leaf temperature is slightly higher than the surrounding air [63]. However, absorption of incident radiation by trichomes can be reduced to 30% to 40% in rain-scarce summer, thus making leaf temperature lower than the surrounding air temperature and this cooling effect of the hairs can increase the gain of carbon and decrease water loss by 20–25% [67]. The specific protection mechanisms require more research to determine the physiological and ecological significance of trichome effects on leaf temperature.

UV protection

Much evidence suggests that trichomes can absorb UV radiation and reduce the damage by UV-B to photosystem II photochemical activity and prevent stomatal closure. Thus, trichomes have a significant

protective effect against UV-B radiation damage in the process of leaf development. Recently, Yan et al. found that exposure of Arabidopsis to UV-B could stimulate trichome formation, and that the UV protection may confer by flavonoids and epidermal waxes in the cell walls of trichomes [68]. The flavonoid substances secreted by trichomes are mainly in the form of water-soluble glycosides in the vacuoles of the epidermal cells of leaves, and are free and lipophilic. The accumulation of flavonoids in the plant epidermis can reduce the transmittance of UV-B radiation in the epidermis layer, and so reduce harm to plant organs and tissues [69]. The reason may be that flavonoids are highly susceptible to O-methylation, thus UV absorption characteristics shift to shorter wavelengths, which can more effectively absorb 250 to 320 nm UV radiations and so reduce the UV-B damage to plants [70]. Because flavonoids can absorb and effectively reduce the amount of UV-B radiation to plant tissue, they play the role of an ‘internal filter’ in plants, and so play an important role in plant biochemical regulation [71].

Drought resistance

The direct result of drought is a lack of available soil moisture, and so leaf transpiration losses exceed water absorption by roots. Morphological anatomical characteristics can enhance drought resistance by alleviating the contradiction between water supply and demand [72]. Shang found that one possible cause of plant drought resistance was the densely velvet trichomes, with the air trapped between the trichomes reducing the transpiration rate without affecting carbon dioxide exchange [63,73]. In addition, trichomes can hinder the proliferation of small pores, thus reducing water loss and playing an important role in water conservation and mitigation of the leaf temperature effect [63,74].

Studies have shown that the proximal and distal (relative to the leaf blade) ends of trichomes may have different effects on moisture retention and water droplets. Fernández et al. [75] examined the physiochemical properties of the proximal and distal ends of soft trichomes and found lower humidity and higher hydrophobicity at the distal end compared to the proximal end near the blade. Importantly, this hydrophobicity was associated with chemical and structural differences in the distal axillary trichomes. However, their analysis concluded that surface chemistry was the driving force for this powerful water–leaf interaction, which increased surface roughness and affected wetting [75]. Although many of the physical and chemical differences in the proximal and distal ends of trichomes and their respective leaf surfaces are not yet clear, the data suggest that trichomes may function differently at their different ends.

Gas exchange of stomata

During the process of aquatic to terrestrial evolution in plants, cuticle and other protective layers appeared to prevent excessive moisture transpiration, and the emergence of a stomatal-intensive gas exchange place, Stomatal and stratum corneum in different growth environments, the formation of the different characteristics of xerophytic plants such as oleander [58,76,77]. In order to prevent excessive transpiration of water, the leaf surface specialization out of the stomatal fossa, stomatal fossa with a number of pores and is covered with epidermal trichomes, so as to protect efficient gas exchange and also to prevent excessive loss of water caused by stomata [78]. The two main resistances in the exchange of gases between plants and the atmosphere are stomatal and boundary layer resistances. Benz and Martin [79] examined the relationships between water and carbon dioxide gas exchange parameters and leaf trichome cover in 12 species of Tillandsia that exhibited a wide range in trichome size and trichome cover and found that trichome-enhanced boundary layers had negligible effects on Tillandsia gas exchange and concluded that

they did not significantly reduce transpirational water loss. However, the trichomes undoubtedly increased the thickness of the boundary layer, the increase due to *Tillandsia* trichomes was inconsequential in terms of whole leaf boundary layers, and any associated reduction in transpirational water loss was also negligible within the whole plant gas exchange pathway [79]. Cai et al. found that a higher net photosynthetic rate was associated with higher stomatal conductance, while the latter might be related to stomatal density and leaf anatomical structure [80].

Insect resistance

Plant trichomes can be a detrimental or beneficial trait to insects, and different insects have different responses. The density, length, softness or hardness, growth direction and shape of trichomes may be related to insect resistance. The mode of action of this insect resistance is rejection, including resistance as habitat (not conducive to insect attachment and movement) and refusing to lay eggs or to eat [81]. The responses of insects to plant burrs of trichomes vary with species, but in general, attachment and action on plant surfaces, feeding and oviposition are affected to varying degrees by trichomes and spines; and when the numbers of trichomes exceeds 300 per unit area, the insects are affected by the trichomes and death [82]. Trichomes can also affect the behavior of certain insect larvae, such as cotton bollworms, by hindering initial incubation on cotton foliage and petioles and exposing them to predators and high temperatures that ultimately lead to exhaustion and death [83]. Trichomes can also affect the digestion of insects with small chewing mouthparts, because the larvae must eat the trichomes to reach the epidermis, and their digestive tract accumulates too many trichomes to be digested [84]. Studies have shown that the density of trichomes on tomato leaves is the main factor leading to insects avoiding plants. In addition, trichomes on the surface of leaves can secrete alkanes, acyl sugars, sesquiterpenes and other chemicals to kill or repel insects [85].

Disease resistance

The trichomes and thorns on plant leaves also play important roles in disease resistance. They can reduce the chance of contact and invasion by suspending pathogen propagules above the leaf surface, and some trichomes can produce toxic substances that inhibit the invasion and germination of pathogen spores [86]. Beckman et al. reported that a phenolic substance was present in the leaves of plants, and was released by external stimuli [87]. Zhenmin et al. found that certain substances from plant trichomes could inhibit the growth of some fungi [88].

Conclusion

Trichomes are widely found on the aerial parts of a range of plants. With the excavation of genes in *Arabidopsis* and *O. sativa*, a series of signaling pathway networks were analyzed. The mechanism of trichome formation in rice differs from that of the dicotyledon *Arabidopsis*. Plant hormones may also be involved in the regulation of trichome formation, which show different regulation mechanisms in different plants. Trichomes begin in seedlings and remain until the plant dies and show the function of the unity of time and space. Moreover, the density, length and distribution of trichomes play corresponding physiological roles in resisting natural stresses because of their specific structure. Further investigating the formation and eco-physiology of trichomes will have important theoretical significance and practical applications.

According to plants growing needs in different ecological regions to improve the environmental adaptability and yield of the plants, we can promote or inhibit the trichomes formation by altering the certain physiological characteristics of trichomes for different plants in the future.

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References

1. Werker E (2000) Trichome diversity and development. *Adv Bot Res* 31: 1-35.
2. Dada O (2013) Growth and stomatal response of *Amaranthus* spp. to different watering regimes, organic and inorganic soil amendments. *Niger J Sci* 47: 15-26.
3. Handley R, Ekbohm B, Agren J (2005) Variation in trichome density and resistance against a specialist insect herbivore in natural populations of *Arabidopsis thaliana*. *Ecol Entomol* 30: 284-292.
4. Yamasaki S, Murakami Y (2014) Continuous UV-B irradiation induces endoreduplication and trichome formation in cotyledons and reduces epidermal cell division and expansion in the first leaves of Pumpkin seedlings. *Environmental Control in Biology* 52: 203-209.
5. Wagner GJ (1991) Secreting glandular trichomes: More than just hairs. *Plant Physiol* 96: 675-679.
6. Wang S, Schiefelbein J (2014) Regulation of cell fate determination in plants. *Front Plant Sci* 5: 368.
7. Zeng YH, Zhu YS, Lian L, Xie HG, Zhang JF, et al. (2013) Genetic analysis and fine mapping of the pubescence gene *GL6* in rice (*Oryza sativa* L.). *Chin Sci Bull* 58: 2992-2999.
8. Theobald WL, Krahulik JL, Rollins RC (1980) Trichome description and classification. *Anatomy of the dicotyledons I*. Clarendon Press: Oxford, pp: 40-53.
9. Barthlott W, Wiersch S, Colic Z, Koch KK (2009) Classification of trichome types within species of the water fern *Salvinia*, and ontogeny of the egg-beater trichomes. *Botany* 87:830-836.
10. Johnson HB (1975) Plant pubescence: An ecological perspective. *The Bot Rev* 41:233-258.
11. Szymanski DB, Jilk RA, Pollock SM, Marks MD (1998) Control of *GL2* expression in *Arabidopsis* leaves and trichomes. *Development* 125: 1161-1171.
12. Kryvykh S, Nikiforova V, Herzog M, Perazza D, Fisahn J, et al. (2008) Gene expression profiling of the different stages of *Arabidopsis thaliana* trichome development on the single cell level. *Plant Physiol Biochem* 46:160-173.
13. Kim HJ, Han JH, Kim S, Lee HR, Shin JS, et al. (2011) Trichome density of main stem is tightly linked to PepMoV resistance in chili pepper (*Capsicum annuum* L.). *Theor Appl Genet* 122: 1051-1058.
14. Ascensão L, Marques N, Pais MS (1995) Glandular trichomes on vegetative and reproductive organs of *Leonotis leonurus* (Lamiaceae). *Ann Bot* 75: 619-626.
15. Brewer CA, Smith WK (1994) Influence of simulated dewfall on photosynthesis and yield in soybean isolines (*Glycine max* [L.] merr. cv Williams) with different trichome densities. *Int J Plant Sci* 460-466.
16. Sun L, Zhang A, Zhou Z, Zhao Y, Yan A, et al. (2015) Glabrous inflorescence stems3 (*GIS3*) regulates trichome initiation and development in *Arabidopsis*. *New Phytol* 206: 220-230.
17. Khosla A, Paper JM, Boehler AP, Bradley AM, Neumann TR, et al. (2014) HD-Zip proteins *GL2* and *HDG11* have redundant functions in *Arabidopsis* trichomes and *GL2* activates a positive feedback loop via *MYB23*. *Plant Cell* 26: 2184-2200.
18. Morohashi K, Zhao M, Yang M, Read B, Lloyd A, et al. (2007) Participation of the *Arabidopsis* bHLH factor *GL3* in trichome initiation regulatory events. *Plant Physiol* 145: 736-746.
19. Chopra D, Wolff H, Span J, Schellmann S, Coupland G, et al. (2014) Analysis of *TTG1* function in *Arabidopsis alpinia*. *BMC Plant Biol* 14: 16.
20. Kirik V, Lee MM, Wester K, Herrmann U, Zheng Z, et al. (2005) Functional diversification of *MYB23* and *GL1* genes in trichome morphogenesis and initiation. *Development* 132:1477-1485.
21. Yu D, Yu F, Du C, Li X, Zhao X, et al. (2015) *RPN1a*, a subunit of the 26S proteasome, controls trichome development in *Arabidopsis*. *Plant Physiol Biochem* 88: 82-88.

22. Qin BX, Tang D, Huang J, Li M, Wu XR, et al. (2011) Rice OsGL1-1 is involved in leaf cuticular wax and cuticle membrane. *Mol Plant* 4: 985-995.
23. Zheng K, Tian H, Hu Q, Guo H, Yang L, et al. (2016) Ectopic expression of R3 MYB transcription factor gene *OstTCL1* in Arabidopsis, but not rice, affects trichome and root hair formation. *Sci Rep* 6: 19254.
24. Schnitger A, Folkers U, Schwab B, Jürgens G, Hülskamp M (1999) Generation of a spacing pattern: The role of Triptychon in trichome patterning in Arabidopsis. *Plant Cell* 11:1105-1116.
25. Wada T, Tachibana T, Shimura Y, Okada, K (1997) Epidermal cell differentiation in Arabidopsis determined by a Myb homolog CPC. *Science* 277:1113-1116.
26. Gan L, Xia K, Chen JG, Wang S (2011) Functional characterization of TRICHOMELESS2, a new single repeat R3 MYB transcription factor in the regulation of trichome patterning in Arabidopsis. *BMC Plant Biol* 11:176 .
27. Tominaga-Wada R, Nukumizu Y (2012) Expression analysis of an R3-Type MYB transcription factor CPC-LIKE MYB4 (Trichomeless 2) and CPL4-related transcripts in Arabidopsis. *Int J Mol Sci* 13: 3478-3491.
28. Kirik V, Simon M, Hülskamp M, Schiefelbein J (2004) The enhancer of TRY and CPC1 gene acts redundantly with triptychon and caprice in trichome and root hair cell patterning in Arabidopsis. *Dev Biol* 268: 506-513.
29. Kirik V, Simon M, Wester K, Schiefelbein J, Hülskamp M (2004) Enhancer of TRY and CPC 2(ETC2) reveals redundancy in the region-specific control of trichome development of Arabidopsis. *Plant Mol Biol* 55: 389-398.
30. Li J, Yuan Y, Lu Z, et al. (2012) Glabrous rice 1, encoding a homeodomain protein, regulates trichome development in rice. *Rice* 5: 1.
31. Iwata N, Omura T, Satoh H (1978) Linkage studies in rice: The sequence of genes at the eighth and eleventh linkage groups. *Jpn J Breeding* 28: 170-171.
32. Yang C, Li H, Zhang J, Luo Z, Gong P, et al. (2011) A regulatory gene induces trichome formation and embryo lethality in tomato. *PNAS* 108: 11836-11841.
33. Guan XY, Li QJ, Shan CM (2008) The HD-Zip IV gene *GaHOX1* from cotton is a functional homologue of the Arabidopsis *GLABRA2*. *Physiologia Plantarum* 134: 174-182.
34. Loguercio LL, Zhang JQ, Wilkins TA (1999) Differential regulation of six novel MYB-domain genes defines two distinct expression patterns in allotetraploid cotton (*Gossypium hirsutum* L.). *Mol Gen Genet* 261: 660-671.
35. Wright RJ, Thaxton PM, El-Zik KM, Paterson AH (1999) Molecular mapping of genes affecting pubescence of cotton. *J Hered* 90: 215-219.
36. Wang S, Wang JW, Yu N, Li CH, Luo B, et al. (2004) Control of plant trichome development by a cotton fiber MYB gene. *The Plant Cell* 16: 2323-2334.
37. Vernoud V, Laigle G, Rozier F, Meeley RB, Perez P, et al. (2009) The HD-ZIP IV transcription factor *OCL4* is necessary for trichome patterning and anther development in maize. *Plant J* 59: 883-894.
38. Moose SP, Lauter N, Carlson SR (2004) The maize macrohairless1 locus specifically promotes leaf blade macro hair initiation and responds to factors regulating leaf identity. *Genetics*, p: 166.
39. Ishida T, Kurata T, Okada K, Wada T (2008) A genetic regulatory network in the development of trichomes and root hairs. *Annu Rev Plant Biol* 59: 365-386.
40. Li J, Yuan Y, Lu Z, Yang L, Gao R, et al. (2012) Glabrous rice 1, encoding a homeodomain protein, regulates trichome development in rice. *Rice (N Y)* 5: 32.
41. Rerie WG, Feldmann KA, Marks MD (1994) The *GLABRA2* gene encodes a home domain protein required for normal trichome development in Arabidopsis. *Genes Brain Behav* 8: 1388-1399.
42. Oppenheimer DG, Herman PL, Sivakumaran S, Esch J, Marks MD (1991) A myb gene required for leaf trichome differentiation in Arabidopsis is expressed in stipules. *Cell* 67: 483-493.
43. Walker AR, Davison PA, Bolognesi-Winfield AC, James CM, Srinivasan N, et al. (1999) The Transparent Testa *Glabra1* locus, which regulates trichome differentiation and anthocyanin biosynthesis in Arabidopsis encodes a WD40 repeat protein. *Plant Cell* 11: 1337-1150.
44. Payne CT, Zhang F, Lloyd AM (2000) *GL3* encodes a bHLH protein that regulates trichome development in Arabidopsis through interaction with *GL1* and *TTG1*. *Genetics* 156: 1349-1362.
45. Zhang F, Gonzalez A, Zhao M, Payne CT, Lloyd A (2003) A network of redundant bHLH proteins functions in all *TTG1*-dependent pathways of Arabidopsis. *Development* 130: 4859-4869.
46. Dubos C, Stracke R, Grotewold E, Weissshaar B, Martin C, et al. (2010) MYB transcription factors in Arabidopsis. *Trends Plant Sci* 15: 573-581.
47. Wang S, Chen JG (2014) Regulation of cell fate determination by single-repeat R3 MYB transcription factors in Arabidopsis. *Front Plant Sci* 5: 133.
48. Dai X, Zhou L, Zhang W, Cai L, Guo H, et al. (2016) A single amino acid substitution in the R3 domain of *GLABRA1* leads to inhibition of trichome formation in Arabidopsis without affecting its interaction with *GLABRA3*. *Plant Cell Environ* 39: 897-907.
49. Luo D, Oppenheimer DG (1999) Genetic control of trichome branch number in Arabidopsis: The roles of the *FURCA* loci. *Development* 126: 5547-5557.
50. Konstantinov DK, Doroshkov AV. The tenth molecular evolutionary evolution of genes related to plant root hair and trichome development.
51. Dobrovolskaya O, Pshenichnikova T, Arbuzeva V, Lohwasser U, Roder M, et al. (2007) Molecular mapping of genes determining hairy leaf character in common wheat with respect to other species of the Triticaceae. *Euphytica* 155: 285-293.
52. Xu X, Dietrich CR, Lessire R, Nikolau BJ, Schnable PS (2002) The endoplasmic reticulum-associated maize *GL8* protein is a component of the acylcoenzyme A elongase involved in the production of cuticular waxes. *Plant Physiol* 128: 924-934.
53. Sturaro M, Hartings H, Schmelzer E, Velasco R, Salamini F, et al. (2005) Cloning and characterization of *GLOSSY1*, a maize gene involved in cuticle membrane and wax production. *Plant Physiol* 138: 478-489.
54. Payne CT, Clement J, Arnold D, Lloyd A (1999) Heterologous MYB genes distinct from *GL1* enhances trichome production when over expressed in *N. tabacum*. *Development* 126: 671-682.
55. Yang C, Li H, Zhang J, Luo Z, Gong P, et al. (2011) A regulatory gene induces trichome formation and embryo lethality in tomato. *PNAS* 108: 11836-11841.
56. Wei J, Yan L, Ren Q, Li C, Ge F, et al. (2013) Antagonism between herbivore-induced plant volatiles and trichomes affects tritrophic interactions. *Plant Cell Environ* 36:315-327.
57. Bickford CP (2016) Eco-physiology of leaf trichomes. *Funct Plant Biol* 43:807-814.
58. Figueiredo AST, Resende JTV, Morales RGF, Goncalves APS, Silva PRD (2013) The role of glandular and non-glandular trichomes in the negative interactions between strawberry cultivars and spider mite. *Arthropod Plant Interact* 7: 53-58.
59. Mershon JP, Becker M, Bickford CP (2015) Linkage between trichome morphology and leaf optical properties in New Zealand alpine *Pachycladon* (Brassicaceae). *NZJ Bot* 53: 175-182.
60. Tattini M, Matteini P, Saracini E, Traversi ML, Giordano C, et al. (2007) Morphology and biochemistry of non-glandular trichomes in *Cistus salvifolius* L. leaves growing in extreme habitats of the Mediterranean basin. *Plant Biol* 9: 411-419.
61. Schreuder MD, Brewer CA, Heine C (2001) Modelled influences of non-exchanging trichomes on leaf boundary layers and gas exchange. *J Theor Biol* 210: 23-32.
62. Karabourniotis G, Papadopoulos K, Papamarkou M, Manetas Y (1992) Ultraviolet-B radiation absorbing capacity of leaf hairs. *Physiol Plantarum* 86: 414-418.
63. Stipanovi RD (1983) Function and chemistry of plant trichomes and glands in insect resistance: protective chemical in plant epidermal glands and appendages, plant resistance to insects. *J Am Chem Soc* 5: 69-100.
64. Hong-Qin S, Jian-Ping L (2010) Comparison of drought resistance of pepper with different hairiness character under drought stress. *J Nucl Agri Sci* 24: 835-839.
65. Hauser MT (2014) Molecular basis of natural variation and environmental control of trichome patterning. *Front Plant Sci* 5: 320.
66. Inomura K, Bragg J, Follows MJ (2017) A Quantitative analysis of the direct and indirect costs of nitrogen fixation: A model based on *A. vinelandii*. *ISME J* 11: 166-175.
67. Lauter DJ, Munns DN (1986) Water loss via the glandular trichomes of chickpea. *J Exp Bot* 37: 640-649.
68. Yan A, Pan J, An L, Gan Y, Feng H (2012) The responses of trichome mutants to enhanced ultraviolet-B radiation in *Arabidopsis thaliana*. *J Photochem Photobiol B* 113: 29-35.
69. Tattini M, Gravano E, Pinelli P, Mulinacci N, Romani A, et al. (2000) Flavonoids

- accumulate in leaves and glandular trichomes of *Phillyrea latifolia* exposed to excess solar radiation. *New Phytol* 148: 69-77.
70. Harborne JB, Williams CA (2000) Advances in flavonoid research since 1992. *Phytochemistry* 55: 481-504.
71. Bin L, Qing Z (2007) Effect of enhanced UV-B radiation on plant flavonoids. *Chinese Journal of Eco-Agriculture* 15: 191-194.
72. Huttunen P, Kärkkäinen K, Loe G, Rautio P, Agren J, et al. (2012) Leaf trichome production and responses to defoliation and drought in *Arabidopsis lyrata* (Brassicaceae). *Ann Acad Sci Fenn* 47: 199-207.
73. Guerfel M, Baccouri O, Boujnah D, Chaïbi W, Zarrouk M, et al. (2009) Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Sci Hort* 119: 257-263.
74. Konrad W, Burkhardt J, Ebner M, Roth-Nebelsick A (2015) Leaf pubescence as a possibility to increase water use efficiency by promoting condensation. *Ecohydrology* 8: 480-492.
75. Fernández V, Sancho-Knapik D, Guzmán P, Peguero-Pina JJ, Gil L, et al. (2014) Wettability, polarity, and water absorption of holm oak leaves: Effect of leaf side and age. *Plant Physiol* 166: 168-180.
76. Ichie T, Inoue Y, Takahashi N, Kamiya K, Kenzo T (2016) Ecological distribution of leaf stomata and trichomes among tree species in a Malaysian lowland tropical rain forest. *J Plant Res* 129: 625-635.
77. Cach-Pérez MJ, Andrade JL, Cetzal-Ix W, Reyes-Garcia C (2016) Environmental influence on the inter- and intra-specific variation in the density and morphology of stomata and trichomes of epiphytic bromeliads of the Yucatan Peninsula. *Bot J Linn Soc* 181: 441-458.
78. Fahn A (1986) Structural and functional properties of trichomes of xeromorphic leaves. *Ann Bot* 57: 631-637.
79. Benz BW, Martin CE (2006) Foliar trichomes, boundary layers and gas exchange in 12 species of epiphytic Tillandsia (Bromeliaceae). *Plant Physiol* 163: 648-656.
80. Cai SH, Li T, Zhou GX, Chen YZ, Wei X, et al. (2016) Gas exchange characteristics in the mangrove associate *Hibiscus tiliaceus*. *Guihaia* 36: 397-404.
81. Dalin P, Ågren J, Björkman C, Huttunen P, Kärkkäinen K, et al. (2008) Leaf trichome formation and plant resistance to herbivory. Induced plant resistance to herbivory. Springer Netherlands.
82. Levin DA (1973) The role of trichomes in plant defense. *Q Rev Biol* 48: 3-15.
83. Eisner T, Eisner M, Hoebeker ER (1998) When defense backfires: Detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. *Proc Natl Acad Sci USA* 95: 4410-4414.
84. Farrar JR, Barbour JD, Kennedy GG (1989) Quantifying food consumption and growth in insects. *Ann Entomol Soc Am* 82: 593-598.
85. Handley R, Ekbohm B, Agren J (2005) Variation in trichome density and resistance against a specialist insect herbivore in natural populations of *Arabidopsis thaliana*. *Ecol Entomol* 30: 284-292.
86. Jingao D, Wufang H (1995) The morphological structures and disease-resistance in plant. *Acta Phytopathologica Sinica* 25: 1-3.
87. Beckman CH, Mueller WC, McHardy WS (1972) The localization of stored phenols in plant hairs. *Physiol Plant Path* 2: 69-74.
88. Zhenmin Y, Junjun D, Heping Y (1996) A preliminary research report on resistance of woolly gene, Tm-2n^v and their recombined genotypes to tomato virus diseases. *Acta Agric Bor Sin* 5: 23-26.

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