

Trichome, a Functional Diversity Phenotype in Plant

Kaizhuan Xiao¹⁻³, Xiaohui Mao^{2-4*}, Yuelong Lin¹⁻³, Huibin Xu^{2,3}, Yonsheng Zhu^{2,3}, Qiuhua Cai^{2,3}, Huaan Xie¹⁻⁴ and Jianfu Zhang^{1-4*}

¹College of Life Science, Fujian Normal University, Fuzhou 350108, Fujian, China

²Rice Research Institute, Fujian Academy of Agricultural Sciences, Fuzhou 350019, Fujian, China

³National Engineering Laboratory of Rice for China, Fuzhou 350003, Fujian, China

⁴Rice Research Institute, Fujian Academy of Agricultural Sciences, Fuzhou 350003, Fujian, China,

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*.

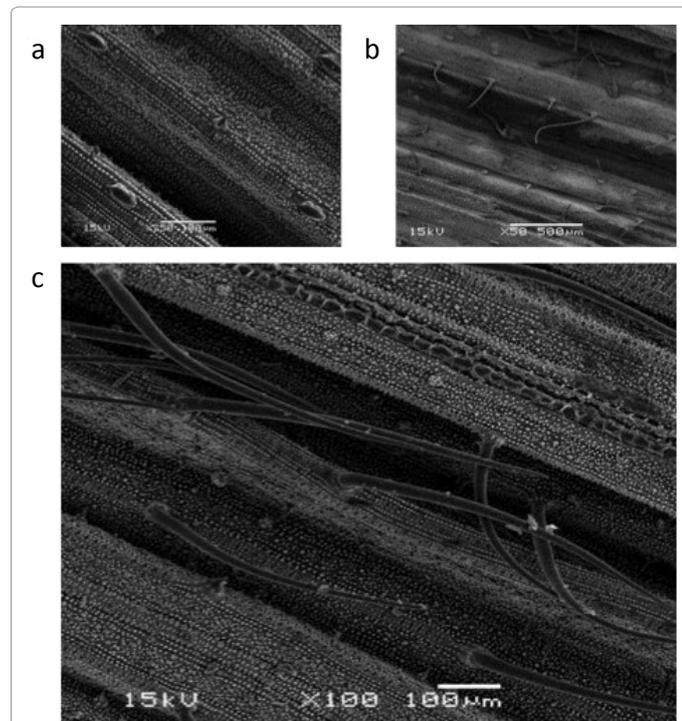


Figure 1: The development of trichome from rice (*Oryza sativa* L.) [7]; a) Trichome morphogenesis at early stages; b) Trichome morphogenesis at middle stages; c) Trichome morphogenesis at mature stages.

***Corresponding author:** Jianfu Zhang, Rice REsearch Institute, Fujian Academy of Agricultural Sciences, Fuzhou 350003, Fujian, China, Tel: 0086-591-83408726, Fax: 0086-591-87868241, E-mail: jianfzhang@163.com

Huaan Xie, Rice Research Institute, Fujian Academy of Agricultural Sciences, Fuzhou 350003

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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

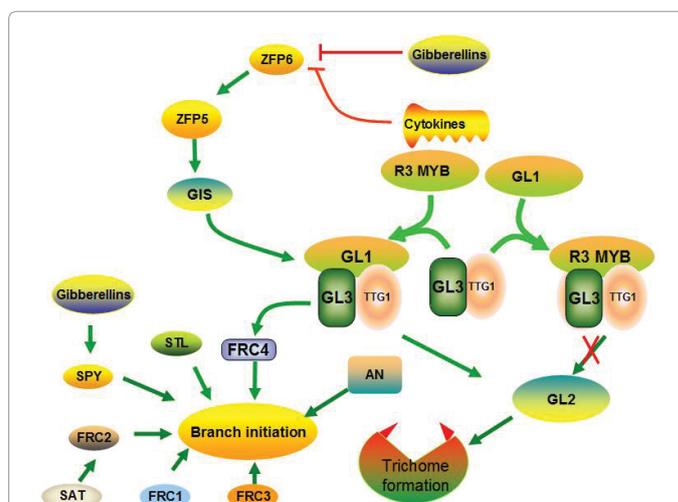


Figure 2: Signaling pathway for the regulation of the trichome in *Arabidopsis thaliana*.

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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