



Review Article

A Review on Epidermal Hair and It's Breeding Project in Plants

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ABSTRACT

Epidermal hair is a specialized structure in the epidermal tissue of plants. Prickles, which are transformed from epidermal hairs and a small number of the cortical cells of plants, are a multicellular and non-glandular type of epidermal hair. This paper reviews the molecular genetic mechanism controlling the development of epidermal hair in plants and prickle-breeding projects. Perspectives on the breeding new types of thornless or less-thorn plants are also offered.

Keyword: Plant epidermal hair; prickles; molecular control; breeding

INTRODUCTION

Epidermal hair is a specialized structure in the epidermal tissue of plants. It develops from epidermic cells and is common in terrestrial plants. Epidermal hair increases the thickness of the epidermal layer of plants, decreases heat and water loss in plants, and protects plants against insect and pathogen attacks as well as mechanical injury [1]. Epidermal hair cells are generally larger than epidermic cells. The former has an average diameter of hundreds of micrometers, with the longest diameter reaching 40–80 μm (e.g., epidermal hair cells of cottonseed). Various types and forms of epidermal hairs have been identified, and these hairs may be classified as glandular or non-glandular hairs based on their secretion ability. Moreover, epidermal hairs can be categorized

as unicellular or multicellular hairs, as well as uniseriate or multiseriate hairs, according to the number and arrangement of cells in the hair. Epidermal hairs can take capitate, star, hook, and scale shapes, among others. Some plants simultaneously grow several types of epidermal hairs. For example, the sea-buckthorn from China presents different types, color, and amounts of epidermal hairs on its different organs [2]. The types, amounts, and sizes of different epidermal hairs are determined by the organs or the surface of the organs (e.g., blades, adaxial side, abaxial side, and stem) that develop these hairs. Various types of epidermal hairs are responsible for the appearance of plants [3]. Blades possessing epidermal hair cells with vacuoles tend to project colors, such

as greyish white, silver, and yellow, because of the different elements in the vacuoles or the effect of refraction.

MOLECULAR GENETIC CONTROL MECHANISM OF EPIDERMAL HAIR DEVELOPMENT

Studies on the molecular genetic control mechanism of the development of epidermal hair in plants have recently shown significant progress. However, relevant studies mainly focus on the model plant, *Arabidopsis thaliana*, which has been thoroughly and intensively examined. *A. thaliana* features unicellular and non-glandular epidermal hair. Over 30 genes controlling the development of epidermal hairs of *A. thaliana* have been identified through genetic analytical methods. Moreover, over 70 mutants responsible for the development of defects in the epidermal hairs of *A. thaliana* have been separated and acquired. These mutants, which involve more than 20 genes, can be classified into six phenotypes, namely, no epidermal hair, fasciation of epidermal hairs, decrease in the amount of hair, epidermal hair distortion, abnormal branching, and vitric epidermal hair [4, 5]. Cloning and studying these controlling genes plays an important role in elucidating the molecular genetic mechanism(s) influencing the initial

developmental phase of epidermal hairs. Several genes that directly control the development of epidermal hairs of *A. thaliana*, such as *GLABROUS1* (*GL1*, belonging to the *MYB* factor family) [6, 7], *TRANSPARENT TESTA GLABRA1* (*TTG1*, *WD40*) [8], *GLABROUS3* (*GL3*, belonging to the *bHLH* factor family) [9], *GLABROUS2* (*HD-ZIP IV* family) [1], *TRANSPARENT TESTA GLABRA2* (belonging to the *WRKY* factor family), *TRIPTYCHON* (belonging to the *MYB* factor family), and *CAPRICE* (belonging to the *MYB* factor family), are transcription factors [11].

The initial developmental phase of epidermal hairs in *A. thaliana* is controlled by *MYB-bHLH-WD40*, a complex consisting of products of at least three genes, namely *GL1*, *GL3*, and *TTG1*. However, whether each of these three genes participates in activating the development of epidermal hairs has not been indicated. Subsequent developmental phases are controlled by *HD-ZIP* factors. *TRICHOMELESS1* (*TCL1*) [12], a member of the *R3MYB* transcription factor family, has been identified in *A. thaliana* and cloned. Overexpression of *TCL1* may lead to the deficiency of epidermal hairs in all organs of *A. thaliana*. Thus, a new controlling factor influencing the development of epidermal hairs has been determined (Fig. 1).

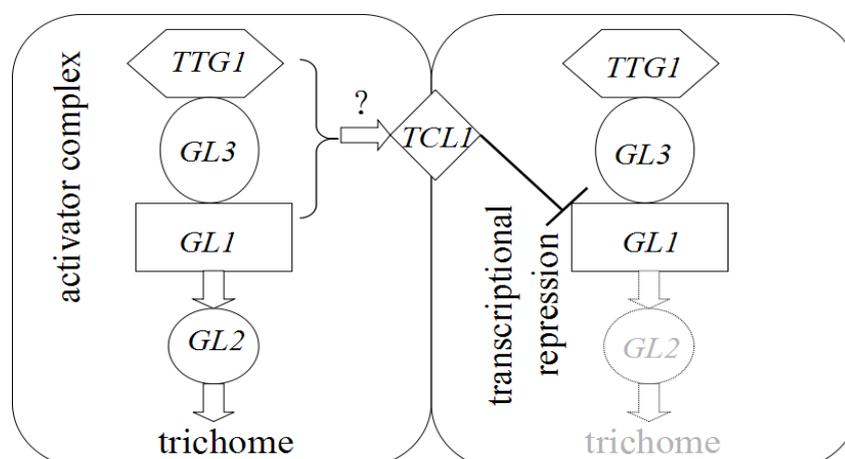


Fig.1: Model of action of *TCL1* in trichome patterning in *Arabidopsis*

Recent studies show that epidermal hair development in most plants shares the same mechanism as that in *A. thaliana*. However, *A. thaliana* may exhibit a developmental mechanism distinct from other plants. Thus, further study should be conducted to elucidate the molecular control mechanism of epidermal hair development of plants differing from that of *A. thaliana*. *GL1*, an R2R3-type coding *MYB* protein[7], is the first gene controlling the initial development of epidermal hairs in *Arabidopsis thaliana* to be cloned. The expression of *gl1*, a mutant of *GL1*, results in the absence of epidermal hair on blades[13]. In 1964, Robinson induced mutation in cucumber by radiation and acquired a mutant cucumber without epidermal hairs. The recessive mutant gene was named *glabrous (gl)*. The mutated cucumber exhibited no epidermal hair on its stem, blade, calyx, ovary, or tendril. In addition, no wart or spine was found on its fruits. Nagata[14] treated different ecological types of *A. thaliana* with γ irradiation to increase the amount of epidermal hair on the plant. However, irradiation did not influence *gl1-1*, which indicates that *GL1* is the key gene controlling the initial development of epidermal hairs on blades. Studies on cucumber show that the presence of epidermal hair on cucumber is controlled by a set of genes, namely, *GL/gl*. Moreover, the presence of hairs is dominant over the absence of hairs. Studies have also located and analyzed *GL*, which induces spine formation on cucumbers [15]. Yang [16] studied *gl-2*, a gene controlling the absence of epidermal hair on cucumbers, using genetic analysis and gene location with screening methods to identify the *gl-2* linkage group, which is built by 18 sets of SSR primers related to *gl-2*, and accurately located the gene on the second chromosome of cucumber. Gene expression profile analysis showed that *GL1* controls the specialized expression of epidermal hairs and only expresses relevant characteristics in epidermal hairs at the starting and other

initial development phases[6]. Overexpression of *GL1* reduces epidermal hairs, which demonstrates that the gene plays a negative role in the initial development of epidermal hairs [17]. This gene also regulates the appropriate expression of *GL2*[18].

TTG1 codes a protein possessing the WD40 repetitive sequence. This highly conserved protein domain is believed to improve the interaction of the protein with other proteins. The influence of the *ttg1* mutant on root hairs and epidermal hairs can be overexpressed through *GL3* and inhibited by the *R bHLH* gene in corn. These phenomena demonstrate that *TTG1* can activate the expression of *GL3* in some pathway and that the normal expression of *GL2* requires the presence of *GL2* in roots and blades. Thus, *TTG1* can interact with the proteins of *GL3* and *GL2*. *TTG1* is a controlling factor that widely exists in plants. This gene participates in the growth and development of plants and expresses itself in major organs of most plants. *TTG1* plays an important role in the formation of epidermal hairs, synthesis of anthocyanidin, formation of meristem, development of the seed coat, and perception and transmission of light signals. The influence of the *ttg1* mutant is not limited to the development of epidermal hairs. This mutant presents several phenotypes, including no epidermal hair on stems or blades, emergence of a large number of ectopic root hairs, and inability to synthesize anthocyanidin. These features induce plants to produce transparent seed coats and yellow cotyledon, the insides of which can be seen through, and prevent the production of mucus for seed coats.

TTG1 is one of the key genes controlling the development of epidermal hairs in *A. thaliana*. Moreover, *ttg1*, the mutant of *TTG1*, may incur function deficiency in *A. thaliana*. The expression of *ttg1* can lead to nearly complete loss of the initially developed epidermal hairs, but its overexpression in wild *A. thaliana* does

not lead to excessive epidermal hairs. In addition, *ttg1* plays an important role in regulating the synthesis of anthocyanidin in *A. thaliana*. The existence of *TTG1*, which has been cloned in various other plants, and relevant study results reveal the importance of this gene. Guan et al. [19] used the *TTG1* gene sequence in cotton and *A. thaliana* to design a primer and conduct homology-based cloning. *CsTTG1*, a gene involved in the formation of spines on cucumber, was eventually identified. RT-PCR results show that this gene expresses itself in major organs and meristems. Functional complementation experiments demonstrate that *CsTTG1* in cucumber is complementary to the *ttg1* mutant in *A. thaliana*. This characteristic shows that the *TTG1* gene in cucumber has functions homologous to those of the *TTG1* gene in *A. thaliana*. Dressel [20] investigated wild and mutated violets with white flowers and without epidermal hairs as experimental materials. *TTG1* genes were acquired and cloned in these plants. Results showed the mutation of a basic group in the nucleotide sequence of the *TTG1* gene in the mutated violets. This basic group mutation resulted in mutation of an amino acid in the *TTG1* gene and induced transformation of tryptophan into arginine, which directly influences the function of the WD gene sequence. Basic group mutation is believed to hinder the protein function of the regulating factors, which interferes with the formation of epidermal hairs, biosynthesis of anthocyanidin, formation of pigment, and development of seed coats. Zhang et al. [21] has built a DH population with a DH line of Chinese cabbages with yellow seeds and no epidermal hair, as well as another DH line of Chinese cabbages with black seeds and epidermal hair as the male parent. By marking relevant genes and using a map-based gene cloning method, the researchers found that the characteristics of epidermal hair presence or absence and the color of seed coat are completely linked with

the *TTG1* gene in *Arabidopsis thaliana*. From the results of complementary experiments conducted on the *ttg1* mutant in *A. thaliana*, researchers found that the *TTG1* gene in the DH line of Chinese cabbages with black seeds and epidermal hair instead of the *TTG1* gene in the other DH line of Chinese cabbages with yellow seeds and no epidermal hair, thus making mutated *A. thaliana* recover the characteristics of wild-type *A. thaliana*. In accordance with the homology theory, Wang et al. [22] designed a primer with the *AtTTG1* gene, which controls the development of epidermal hair on *A. thaliana*, and cloned the *NtTTG1* gene, which is involved in epidermal hair development in tobacco. From the results of years of two hybrid experiments, researchers found that the protein encoded by *NtTTG1* is in cross interaction with the protein elicitor of *Para1*, which is secreted by oomycetes. In addition, aided by RT-PCR reaction and RACE technology, researchers cloned *NtTTG1-like*, a new gene for tobaccos, and acquired the silencing plant of the gene, thereby laying a solid foundation for further study on the development of tobacco epidermal hair and relevant functions of these epidermal hair.

GL3 encodes *bHLH* protein and regulates the morphogenesis and normal specialization of epidermal hair. For "Landsberg", an ecotype of *A. thaliana*, the formation of epidermal hair of the mutant *gl3* is less influenced than those of *ttg1* and *gl1*. The epidermal hair of *gl3* is not lost completely, but decreases in number and incompletely develops, with no or few branches. The interaction between the proteins of *GL3* and *GL1* promotes the overexpression of *GL3* and *GL1* and increases the number of epidermal hair, indicating that the development of epidermal hair depends on the interaction of *GL1* and *GL3*. Zhang et al. [23] found out that the expression quantity of *GL3* in epidermal cells of developing spires is extremely low. Epidermal hair development increases but decreases to a low level again in the epidermal

cells of mature blades or mature epidermal hair. This finding demonstrates that, along with other genes, *GL3* regulates the development of epidermal hair and can sometimes work with functional redundancy.

GL2, a kind of homeobox gene, encodes a kind of transcription factor. This transcription factor type contains HD-ZIP and expresses itself during the whole development process of epidermal hair [1,10]. This factor is necessary for the specialization and differentiation of non-root hair and epidermal hair. Through genetic analysis, researchers found that *GL2* functions on the downstream part of *TTG1* and *GL1* [10]. The expression quantity of *GL2* in *gl3*, *gl1*, and *ttg1* decreases to a large extent, indicating that *GL3*, *TTG1*, and *GL1* regulate the expression of *GL2* in epidermal hair [17].

BREEDING PROJECT ON PLANT EPIDERMAL HAIR

Epidermal hairs (prickles) are unnecessary for certain parts (for example, fruits and stems) of plants to defend themselves against natural enemies that eat them. However, these hair cause inconvenience to plant cultivation and management, as well as the collection, transportation, and processing of fruits. Numerous prickles are found on the stems of various *Rosa* plants and do not fall off, engendering considerable inconvenience to relevant processing and transportation. Taking roses as an example, prickles on roses may cause injuries to machines during processing and transportation. Removal of prickles through mechanical measures may cause injury to the plant and narrow its life span. In addition, prickles are needle-like, thus making the removal process complicated and difficult and consequently incurring the considerable waste of manpower and material resources. For improvement of the characteristics of plants through cross breeding, as well as haploid and polyploid breeding, molecular breeding, in-vitro culture technique, and other methods are used

to breed and cultivate new varieties of plants with few or no hair (or spine). These approaches can not only promote the production and processing of these plants to increase economic profits but also enrich the genetic resources of plants.

Prickle, which is transformed from epidermal hair and a small number of cortical cells of plants, is a special form of epidermal hair that is multicellular and glandless. Prickles are a type of speculate tubers that develop from the cortex or epidermal cells on stems and branches and scatter on stems irregularly. Prickles are developed at the epithelial layer and are not attached to the xylem. Thus, stripping these sections off from plants is easy. A smooth and flat section is revealed after the prickles are stripped off. Prickles are commonly seen in plants. Families Rosaceae, Araliaceae, Rutaceae, and Leguminosae comprise the most common plants exhibiting prickles, such as *Rosa rugosa*, *Rosa chinensis*, *Rosa multiflora*, *Zanthoxylum bungeanum*, and *Aralia chinensis*. Prickles grow not only on stems and branches but also on leaves or fruits. For example, urticaceous plants are covered with prickles on their entire body surface. The petioles and leaf veins of wild nightshades grow prickles. The petioles of raspberries and the back side of their leaves exhibit numerous small prickles. The surface of wintersweet leaves are covered with a layer of tiny barbs. The fruits of some plants, such as caltrops in the caltrop family, daturas in Solanaceae, and Roxburgh rose in Saxifragaceae, show prickles on their surfaces. Some plants, including chestnuts and *Onopordum acanthium*, burdocks, and *Xanthium strumarium*, develop spiculate prickles specialized from involucre. In other plants, such as agrimonies in Rosaceae, prickles grow on calyx edges [24].

At present, studies have achieved considerable progress in epidermal hair breeding. Wei et al. bred the Q1038 strain from fluffy cotton plants [25]. Plants of this new strain of upland cotton

are characterized by their lack of epidermal hair. This absence of hair is a stable attribute; except for a few tomenta scattered on leaf margins and petioles, nearly no hair can be found on all of the other plant organs. Blades are also completely devoid of epidermal hair. Through over five years of cultivation experiments, scholars have proven that the fiber of plants of the Q1038 strain is of good quality. Moreover, the plants themselves show substantial yielding ability. Plants of the new strain demonstrate good resistance against pink bollworms, significantly decreasing economic loss from insect infestation. Through artificial hybridization, Guo et al. [26] bred and selected "Bosom Friend," a new variety of Chinese rose without epidermal hair. Utilizing years of research on rapid breeding technology, the scholars created a new seedling cultivation method that enabled grafting of tender shoots on the top of twigs and plump shoots as scions to the middle portion of twigs. Liang et al. [27] bred and selected a new variety of Chinese rose named "Proud Snow" from filial generations of "Christmas Snow." The flowers of this new variety are of pure white, small, and arranged in a compact manner. The sprays are long, straight, smooth, and show virtually no spines. Plants of this new variety could provide suitable cut flowers. Later generations bred through cutting and grafting exhibited the same stable characteristics as their female parents. Studies have proven that this new variety presents substantial resistance against black spot disease. By adopting the common tissue culture technique, Ken et al. [28] bred a new spineless blackberry variety called "Four Seasons without Spine" (lacking spines on the root seedlings and inner tissues of stems) isolated and selected from another blackberry variety called "Evergreen and Spineless" (lacking spines on stems but not on root seedlings and shoots; this variety was developed using genes in inner tissues controlling the spine-producing trait). Field experiment results showed that the plants

of this new variety exhibit considerable yielding ability with high-quality fruits. The new plants obtained were also dwarfs, thereby facilitating cultivation and management. Japanese spineless ash exhibit the desirable attribute of complete absence of spines. This characteristic enables the easy management and fruit collection of Japanese spineless ash trees. Chen et al. [29] obtained current-year stems with buds acquired from Japanese spineless ash as explants and conducted tissue culture to study the rapid propagation technique of this variety. The results of their study showed that modified MS induction medium can multiply explants rapidly and that transplanted Japanese spineless ash exhibit a high survival rate. The fruits of a new variety of *Rosa kweichonensis* var. *sterilis* with smooth branches can be eaten without cooking. Because these fruits lack seeds and are palatable and nutritious, this variety has been paid close attention both locally and abroad. Over three years of introduction and domestication, as well as propagation experimentation, An et al. [30] proved that the twigs and petioles of this new variety are smooth and lack epidermal hair. This variety was also found to be a good climbing shrub with rapid growth, easy propagation, high stress resistance, and strong adaptive capacity.

PERSPECTIVE

Although great progress has been achieved in cultivating new varieties of plants by exploiting their epidermal hair traits, scholars have not elucidated the mechanisms underlying the developmental phase this plant component. Research on the epidermal hair development of useful plants and crops is rare. In addition, little is known about the relationship between epidermal hair development and plant reactions to stress. Cultivation of new crop varieties with few or no hairs (or spines) can significantly improve the efficiency of agricultural work, including field management and flower collection. Even so, further studies

are necessary to determine whether these new varieties could generate opposite effects if cultivated blindly.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

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