

Involvement of C₂H₂ zinc finger proteins in the regulation of epidermal cell fate determination in *Arabidopsis*

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Minireview



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Abstract Cell fate determination is a basic developmental process during the growth of multicellular organisms. Trichomes and root hairs of *Arabidopsis* are both readily accessible structures originating from the epidermal cells of the aerial tissues and roots respectively, and they serve as excellent models for understanding the molecular mechanisms controlling cell fate determination and cell morphogenesis. The regulation of trichome and root hair formation

is a complex program that consists of the integration of hormonal signals with a large number of transcriptional factors, including MYB and bHLH transcriptional factors. Studies during recent years have uncovered an important role of C₂H₂ type zinc finger proteins in the regulation of epidermal cell fate determination. Here in this minireview we briefly summarize the involvement of C₂H₂ zinc finger proteins in the control of trichome and root hair formation in *Arabidopsis*.

Keywords: C₂H₂; cell fate determination; root hair; trichome; zinc finger protein

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INTRODUCTION

For a single zygote to develop into an integrated multicellular plant, it must undergo a complex array of cell divisions, cell enlargement, and cell specification (Zhao et al. 2012; Wang et al. 2013). How cells develop into different types and what determines the kind of fate a cell will adopt remain fundamental issues of great importance. Cell differentiation is a complex process subject to exquisite spatial and temporal regulation, and the developmental programs together with positional information provide the pivotal controls for this event (Kang et al. 2013). In recent decades, *Arabidopsis* trichomes and root hairs have been proved to be ideal models for the study of the molecular mechanism of epidermis cell fate determination and cell differentiation (Szymanski et al. 2000; Ishida et al. 2008; Tominaga-Wada et al. 2011; Yang and Ye 2013).

Arabidopsis trichomes are large unicellular structures originating from the epidermal cells of aerial organs of plants, and they are regularly distributed on the organ surface in a particular pattern (Szymanski et al. 2000; Ishida et al. 2008). Trichomes provide physical protection against insects and pathogen intrusion for plants, and they function as a natural shield against detrimental abiotic stress such as drought and

UV radiation damage (Levin 1973; Yan et al. 2012; Yang and Ye 2013). Whether an epidermal cell chooses to develop into a trichome cell or a non-trichome (pavement) cell is exquisitely controlled (Larkin et al. 1996; Telfer et al. 1997). To date, extensive studies have identified a large number of regulatory genes/proteins involved in trichome initiation and morphogenesis. A core combinatorial regulatory complex is formed by the GLABRA1 (GL1), GLABRA3 (GL3)/ENHANCER OF GLABRA3 (EGL3), and TRANSPARENT TESTA GLABRA1 (TTG1), which are R₂R₃ MYB transcription factors, bHLH transcription factors, and WD40 repeat protein, respectively (Oppenheimer et al. 1991; Hülskamp et al. 1994; Walker et al. 1999; Payne et al. 2000; Szymanski et al. 2000; Ishida et al. 2008; Zhao et al. 2008). This regulatory complex acts upstream of the GLABRA2 (GL2) gene to promote trichome initiation (Ishida et al. 2008; Zhao et al. 2008). In contrast, several negative regulators have also been identified, which act as inhibitors of trichome formation in neighboring cells. These include CAPRICE (CPC) (Wada et al. 1997), TRIPTYCHON (TRY) (Schellmann et al. 2002), ENHANCER OF TRY AND CPC 1 (ETC1) and ETC2 (Kirik et al. 2004a, 2004b), which are all truncated versions of MYB transcription factors. Because they lack a putative transcriptional activation domain but possess a GL3/EGL3-binding domain, these negative regulators

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appear to interfere with the formation of the GL1-GL3/EGL3-TTG regulatory complex (Esch et al. 2003; Wester et al. 2009).

Root hairs are long tubular-shaped outgrowths differentiating from root epidermal cells (Gilroy and Jones 2000; Grierson and Schiefelbein 2002). Root hairs are essential for root anchorage in soil and effectively enhance the uptake of nutrient and water as they markedly increase the root surface area (Gilroy and Jones 2000; Lucas et al. 2013). In *Arabidopsis*, root hairs are produced by epidermal cells located outside a cortical cell boundary (H cells), while other epidermal cells are defined as non-hair cells (N cells) (Schiefelbein et al. 2009; Löffke et al. 2013). Like trichome development, root hairs are specified using similar regulatory proteins. The TTG1, GL2, GL3, EGL3, WEREWOLF (WER) (Lee and Schiefelbein 1999), and MYB23 (Kang et al. 2009) act as positive regulators in the N cells to promote the non-hair cell fate specification (Ishida et al. 2008), while CPC, TRY, and ETC1 are produced in N cells but move to neighboring H cells where they compete with WER for binding to the GL3/EGL3-TTG1 complex and thereby maintain the H cell fate (Ishida et al. 2008; Bruex et al. 2012; Kang et al. 2013). Collectively, MYB transcription factors and bHLH transcription factors play the central role in controlling trichome and root hair cell fate determination. In addition to the MYB and bHLH transcription factors, C2H2 type zinc finger proteins have been found to participate in epidermal cell type specification in recent years (Gan et al. 2006, 2007a; Zhou et al. 2011, 2013; An et al. 2012b). Here we briefly summarize the involvement of the novel C2H2 zinc finger proteins in the regulation of trichome and root hair formation in *Arabidopsis*.

C2H2 ZINC FINGER PROTEIN IN PLANTS

Zinc finger proteins are a large class of proteins that are widely distributed in eukaryotes (Laity et al. 2001). They are among the most abundant proteins in eukaryotic organisms, indicative of the involvement of zinc finger proteins in a wide range of cellular functions, including DNA recognition, RNA binding, transcriptional regulation, and protein-protein interactions (Laity et al. 2001; Ciftci-Yilmaz and Mittler 2008). Zinc finger proteins contain sequence motifs in which the cysteines and histidines residues center on a zinc ion to form a compact finger structure, which constitutes the basis for protein functions (Miller et al. 1985; Takatsuji 1998). According to the number and order of the Cys and His residues that bind the zinc ion, zinc finger proteins are divided into several different types including C2H2, C2C2, C2HC, C2C2C2C2, and C2HCC2C2 (Ciftci-Yilmaz and Mittler 2008). Among these distinct types of zinc finger proteins, the C2H2-type zinc finger proteins are one of the largest transcriptional factor families in plants, with 176 members in *Arabidopsis* identified through *in silico* analysis (Englbrecht et al. 2004; Ciftci-Yilmaz and Mittler 2008). To date, C2H2 zinc finger proteins have been found to participate in extraordinarily diverse signal transduction pathways and developmental processes, including flower development (Bowman et al. 1992; Sakai et al. 1995; Yun et al. 2002; Xiao et al. 2009), seed and seedling development (Luo et al. 1999; Prigge and Wagner 2001), trichome and root hair formation (Gan et al. 2006, 2007a; Zhou et al. 2011, 2013; An et al. 2012b), pathogen defense (McGrath et al. 2005; Kazan 2006; Wang

et al. 2009), and stress responses (Kazan 2006; Sun et al. 2010; Tian et al. 2010; Kiełbowicz-Matuk 2012; Zhang et al. 2012).

C2H2 ZINC FINGER PROTEINS ARE INVOLVED IN TRICHOME AND ROOT HAIR FORMATION AND DEVELOPMENT

Although MYB and bHLH transcriptional factors constitute the core regulatory complex in the control of epidermal cell specification, other regulators like C2H2 zinc finger proteins also play important roles in this program. The first-reported C2H2 zinc finger transcription factor that is involved in epidermal differentiation is GLABROUS INFLORESCENCE STEMS (GIS), which also participates in the regulation of shoot maturation in *Arabidopsis* (Gan et al. 2006). The lack of GIS function in *gis* mutants results in a striking decrease in trichome number on successive leaves, stem internodes, and branches, while overexpression of GIS causes the opposite outcome. GIS is strongly expressed in the stem epidermis and in floral meristems. Molecular and genetic analysis show that GIS acts upstream of the trichome initiation complex (GL1-GL3-TTG1) to promote inflorescence trichome initiation in a GA-responsive pathway that is negatively regulated by the GA signaling repressor SPINDLY (SPY) and DELLA repressor GAI (Gan et al. 2006). GIS is also found to function as a repressor in controlling trichome branching by acting downstream of the key regulators of trichome branching *STICHEL* (*STI*) and *SIAMESE* (*SIM*), and the performance of GIS in this scenario is manipulated partly in a GA-dependent manner (An et al. 2012a; Sun et al. 2013).

Further studies defined two homologs of GIS that participate in the determination of epidermal cell fate in *Arabidopsis* via phylogenetic analyses (Figure 1), ZINC FINGER PROTEIN 8 (*ZFP8*) and GLABROUS INFLORESCENCE STEMS 2 (*GIS2*), which encode C2H2 transcription factors functionally equivalent to GIS (Gan et al. 2007a). A *zfp8* loss-of-function mutant exhibits a significant reduction in trichome density on upper cauline leaves and branches, while the *gis2* mutant shows a very strong decrease in trichome production on flowers. Quantitative RT-PCR analysis showed that expression of *ZFP8* and *GIS2* are both GA-inducible; moreover, expression of *GIS2* is also cytokinin-inducible. Both GA and cytokinins are able to promote trichome formation in *Arabidopsis* (Perazza et al. 1998; Greenboim-Wainberg et al. 2005; An et al. 2011). Accordingly, *ZFP8* and *GIS2* were found to be required for GA-mediated regulation of trichome initiation throughout inflorescence development, like their homologs GIS, and their gene expression is repressed by the DELLA repressors GAI, RGA, RGL1 and RGL2 (Gan et al. 2007b). In contrast to GIS, *ZFP8* and *GIS2* are both involved in the cytokinins-mediated induction of trichome initiation on inflorescence organs; furthermore, *GIS2* plays a predominant role in the cytokinin response by acting downstream of SPINDLY to activate *GL1* transcription (Gan et al. 2007b).

Recently, a new C2H2 transcriptional factor, ZINC FINGER PROTEIN 5 (*ZFP5*), was discovered as a positive regulator of trichome initiation through GA signaling pathway in *Arabidopsis* (Zhou et al. 2011). *ZFP5* loss-of-function mutations lead to a significant decrease in trichome number on sepals, cauline

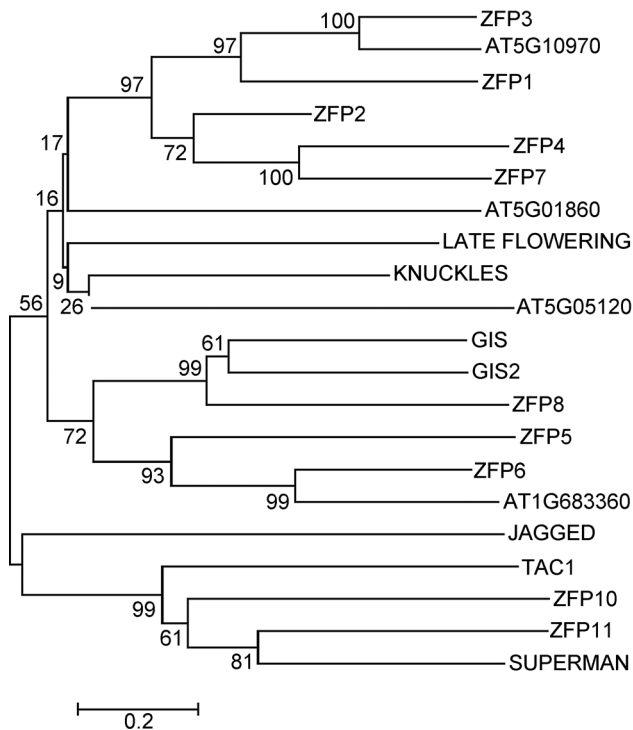


Figure 1. Phylogenetic tree of C2H2 zinc finger proteins whose amino sequences are similar to GLABROUS INFLORESCENCE STEMS (GIS)

The tree was generated using the neighbor-joining method (Saitou and Nei 1987) in MEGA 5 (Tamura et al. 2011). The number of bootstrap replications was set at 1,000. Bootstrap values are provided near the nodes.

leaves, paraclades, and main inflorescence stems, while overexpression of *ZFP5* results in high density of trichomes on the second lateral branch and inflorescence organs (Zhou et al. 2011). Moreover, *ZFP5* overexpression causes the formation of ectopic trichomes on carpels, petals, and other inflorescence organs (Zhou et al. 2011). Molecular analyses demonstrated that *ZFP5* acts upstream of *GIS*, *GIS2*, *ZFP8*, and the key members of trichome initiation complex *GL1* and *GL3* to promote trichome initiation. Further chromatin immunoprecipitation (ChIP) analysis confirmed that *ZFP8* is the direct target of *ZFP5*. More detailed data indicated that *ZFP5* is functionally equivalent to *GIS* and *GIS2* in controlling trichome initiation (Zhou et al. 2012). These results are consistent with previous phylogenetic analysis that showed *GIS* is most highly related to the ZFP group of transcription factors, of which *ZFP5* and *ZFP8* are the most similar to *GIS* (Figure 1) (Gan et al. 2006).

ZFP5 is highly expressed in roots, developing stems, branches, and young leaves (Zhou et al. 2011), so it was reasonable to consider that *ZFP5* may also function in root epidermal cell differentiation. Indeed, further experiments confirmed that *ZFP5* is a key regulator of root hair initiation and morphogenesis in *Arabidopsis* (An et al. 2012b). The *zfp5* mutants and *ZFP5* RNAi lines have fewer and much shorter root hairs, and in situ RNA hybridization assays showed that *ZFP5*

was mainly expressed in the H cells of the root epidermis. Molecular and genetic analyses revealed that *ZFP5* is likely to act upstream of the CPC-TRY-ETC1 complex to promote the activity of the complex via directly binding to the CPC promoter. Moreover, *ZFP5* expression is cytokinin-inducible, and *ZFP5* is required for cytokinin and ethylene signals to control root hair development (An et al. 2012b). Collectively, *ZFP5* integrates various plant hormone signaling to control trichome and root hair formation and development in *Arabidopsis* (Zhou et al. 2011; An et al. 2012b).

Most recently, ZINC FINGER PROTEIN 6 (*ZFP6*) has been found to be another C2H2 transcriptional factor involved in the regulation of trichome initiation (Zhou et al. 2013). Amino acid sequence analysis revealed that *ZFP6*, a member of the *GIS* subfamily, is most similar to *ZFP5* among the ZFP group of transcription factors (Gan et al. 2006). With similar expression pattern to *ZFP5*, *ZFP6* is highly expressed in roots, mature stem and lateral branches. The *zfp6* mutant shows a reduced number of trichomes in sepals of flowers, cauline leaves, lateral branches, and the main inflorescence stems (Zhou et al. 2013). In contrast, *ZFP6* overexpression increases trichome numbers in second cauline leaves, second lateral branches and the main inflorescence stem, and it causes ectopic trichome formation on carpels and petals (Zhou et al. 2013). *ZFP6* also modulates the regulation of trichome cell differentiation during inflorescence development by GA and cytokinin signaling, similar to *ZFP5*. Molecular studies demonstrated that *ZFP6* acts upstream of the *ZFP5* and *GIS* in the trichome regulatory network.

Collectively, the results obtained so far lead us to a regulatory network model that proposes C2H2 zinc finger proteins play partially redundant and distinct roles in the

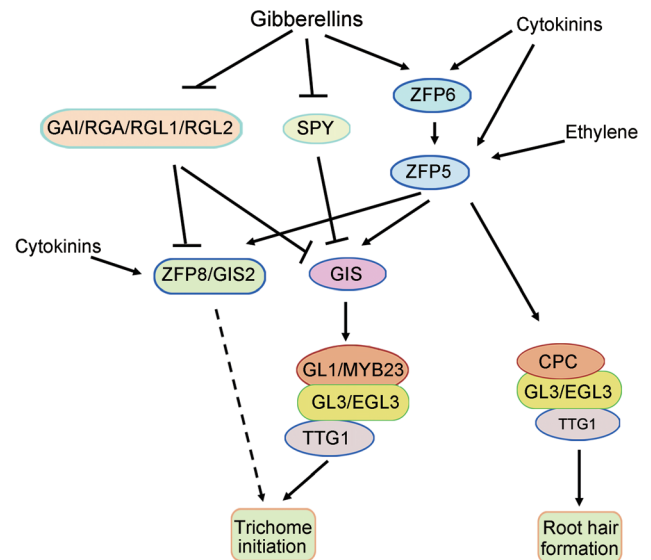


Figure 2. Proposed model of the action of C2H2 zinc finger proteins in the regulation of trichome and root hair formation in *Arabidopsis*

Arrows indicate positive regulation and T-bars indicate negative regulation. Dotted arrows indicate relationships that have not been fully characterized.

control of trichome and root hair cell differentiation (Figure 2). Among all five identified C2H2 zinc finger transcriptional factors, it is clear that GIS, ZFP5, and ZFP6 promote trichome initiation by functioning as transcriptional activators located upstream of trichome initiation complex (GL1-GL3-TTG1). In addition, GIS2 and ZFP8 work synergistically with GIS to control trichome initiation in inflorescence in *Arabidopsis*, whereas their downstream regulatory network remains obscure (Gan et al. 2007a). Abundant evidence also provides new insight into our understanding of how C2H2 zinc finger proteins integrate various hormonal and developmental cues to control epidermal cell fate determination in *Arabidopsis*.

CONCLUSIONS AND FUTURE PERSPECTIVES

Although C2H2 zinc finger proteins constitute one of the most abundant families of transcriptional regulators in plants, the discovery of a role for C2H2 zinc finger proteins in control of epidermal cell fate determination has only emerged in the last decade. GIS, GIS2, and ZFP8 function equivalently and appear to be functionally interchangeable in the control of trichome initiation, although they diverge in their responses to hormonal and developmental signals. ZFP6 mediates the regulation of trichome initiation by integrating GA and cytokinin signaling in a similar way with ZFP5, but these function separately as no additive effect was found in *zfp5zfp6* double mutants. These observations lead us to conclude that functional specialization of phylogenetically related transcription factor genes is important in coordinating the integration of various hormonal and developmental cues to regulate similar developmental programs at different stages and different tissues.

Future studies will likely focus on the precise mechanisms through which developmental and hormonal signals are integrated to control epidermal cell fate determination in plants, as how phytohormone signaling pathways coordinate various transcriptional regulators in this process still remain largely obscure. Meanwhile, although some C2H2 zinc finger proteins play important roles in epidermal cell fate determination, there are still many C2H2 zinc finger proteins whose biological functions are unknown. With the rapid emergence of new experimental technologies, such as ChIP-seq and systems biology approaches, our knowledge of the C2H2 zinc finger protein family and other transcriptional factor families will be enriched. The integration of these regulators with developmental and hormonal cues will ultimately lead to a complete picture of how phytohormone signals coordinate diverse transcriptional factors to control epidermal cell fate determination in plants.

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REFERENCES

- An L, Zhou Z, Su S, Yan A, Gan Y (2012a) GLABROUS INFLORESCENCE STEMS (GIS) is required for trichome branching through gibberellin acid signaling in *Arabidopsis*. *Plant Cell Physiol* 53: 457–469
- An L, Zhou Z, Sun L, Yan A, Xi W, Yu N, Cai W, Chen X, Yu H, Schiefelbein J (2012b) A zinc finger protein gene *ZFP5* integrates phytohormone signaling to control root hair development in *Arabidopsis*. *Plant J* 72: 474–490
- An L, Zhou Z, Yan A, Gan Y (2011) Progress on trichome development regulated by phytohormone signaling. *Plant Signal Behav* 6: 1–4
- Bowman JL, Sakai H, Jack T, Weigel D, Mayer U, Meyerowitz EM (1992) SUPERMAN, a regulator of floral homeotic genes in *Arabidopsis*. *Development* 114: 599–615
- Bruex A, Kainkaryam RM, Wieckowski Y, Kang YH, Bernhardt C, Xia Y, Zheng X, Wang JY, Lee MM, Benfey P, Woolf PJ, Schiefelbein J (2012) A gene regulatory network for root epidermis cell differentiation in *Arabidopsis*. *PLoS Genet* 8: e1002446
- Ciftci-Yilmaz S, Mittler R (2008) The zinc finger network of plants. *Cell Mol Life Sci* 65: 1150–1160
- Englbrecht CC, Schoof H, Böhm S (2004) Conservation, diversification and expansion of C2H2 zinc finger proteins in the *Arabidopsis thaliana* genome. *BMC Genomics* 5: 39
- Esch JJ, Chen M, Sanders M, Hillestad M, Ndkium S, Idelkope B, Neizer J, Marks MD (2003) A contradictory *GLABRA3* allele helps define gene interactions controlling trichome development in *Arabidopsis*. *Development* 130: 5885–5894
- Gan Y, Kumimoto R, Liu C, Ratcliffe O, Yu H, Broun P (2006) GLABROUS INFLORESCENCE STEMS modulates the regulation by gibberellins of epidermal differentiation and shoot maturation in *Arabidopsis*. *Plant Cell* 18: 1383–1395
- Gan Y, Liu C, Yu H, Broun P (2007a) Integration of cytokinin and gibberellin signalling by *Arabidopsis* transcription factors GIS, ZFP8 and GIS2 in the regulation of epidermal cell fate. *Development* 134: 2073–2081
- Gan Y, Yu H, Peng J, Broun P (2007b) Genetic and molecular regulation by DELLA proteins of trichome development in *Arabidopsis*. *Plant Physiol* 145: 1031–1042
- Gilroy S, Jones DL (2000) Through form to function: Root hair development and nutrient uptake. *Trends Plant Sci* 5: 56–60
- Greenboim-Wainberg Y, Maymon I, Borochoy R, Alvarez J, Olszewski N, Ori N, Eshed Y, Weiss D (2005) Cross talk between gibberellin and cytokinin: The *Arabidopsis* GA response inhibitor SPINDLY plays a positive role in cytokinin signaling. *Plant Cell* 17: 92–102
- Grierson C, Schiefelbein J (2002) Root hairs. *The Arabidopsis Book*. American Society of Plant Biologists, Rockville. pp. 1–22
- Hülkamp M, Miséra S, Jürgens G (1994) Genetic dissection of trichome cell development in *Arabidopsis*. *Cell* 76: 555–566
- 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
- Kang YH, Kirik V, Hülkamp M, Nam KH, Hagely K, Lee MM, Schiefelbein J (2009) The MYB23 gene provides a positive feedback loop for cell fate specification in the *Arabidopsis* root epidermis. *Plant Cell* 21: 1080–1094

- Kang YH, Song S-K, Schiefelbein J, Lee MM (2013) Nuclear trapping controls the position-dependent localization of CAPRICE in the root epidermis of *Arabidopsis*. **Plant Physiol** 163: 193–204
- Kazan K (2006) Negative regulation of defence and stress genes by EAR-motif-containing repressors. **Trends Plant Sci** 11: 109–112
- Kiełbowicz-Matuk A (2012) Involvement of plant C₂H₂-type zinc finger transcription factors in stress responses. **Plant Sci** 185–186: 78–85
- Kirik V, Simon M, Huelskamp M, Schiefelbein J (2004a) 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
- Kirik V, Simon M, Wester K, Schiefelbein J, Huelskamp M (2004b) 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
- Laity JH, Lee BM, Wright PE (2001) Zinc finger proteins: New insights into structural and functional diversity. **Curr Opin Struct Biol** 11: 39–46
- Larkin JC, Young N, Prigge M, Marks MD (1996) The control of trichome spacing and number in *Arabidopsis*. **Development** 122: 997–1005
- Lee MM, Schiefelbein J (1999) WEREWOLF, a MYB-related protein in *Arabidopsis*, is a position-dependent regulator of epidermal cell patterning. **Cell** 99: 473–483
- Levin DA (1973) The role of trichomes in plant defense. **Q Rev Biol** 48: 3–15
- Löfke C, Dünser K, Kleine-Vehn J (2013) Epidermal patterning genes impose non-cell autonomous cell size determination and have additional roles in root meristem size control. **J Integr Plant Biol** 55: 864–875
- Lucas WJ, Groover A, Lichtenberger R, Furuta K, Yadav S-R, Helariutta Y, He XQ, Fukuda H, Kang J, Brady SM, Patrick JW, Sperry J, Yoshida A, López-Millán AF, Grusak MA, Kachroo P (2013) The plant vascular system: Evolution, development and functions. **J Integr Plant Biol** 55: 294–388
- Luo M, Bilodeau P, Koltunow A, Dennis ES, Peacock WJ, Chaudhury AM (1999) Genes controlling fertilization-independent seed development in *Arabidopsis thaliana*. **Proc Natl Acad Sci USA** 96: 296–301
- McGrath KC, Dombrecht B, Manners JM, Schenk PM, Edgar CI, Maclean DJ, Scheible W-R, Udvardi MK, Kazan K (2005) Repressor-and activator-type ethylene response factors functioning in jasmonate signaling and disease resistance identified via a genome-wide screen of *Arabidopsis* transcription factor gene expression. **Plant Physiol** 139: 949–959
- Miller J, McLachlan A, Klug A (1985) Repetitive zinc-binding domains in the protein transcription factor IIIA from *Xenopus oocytes*. **EMBO J** 4: 1609–1614
- 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
- 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
- Perazza D, Vachon G, Herzog M (1998) Gibberellins promote trichome formation by up-regulating GLABROUS1 in *Arabidopsis*. **Plant Physiol** 117: 375–383
- Prigge MJ, Wagner DR (2001) The *Arabidopsis* SERRATE gene encodes a zinc-finger protein required for normal shoot development. **Plant Cell** 13: 1263–1280
- Saitou N, Nei M (1987) The neighbor-joining method: A new method for reconstructing phylogenetic trees. **Mol Biol Evol** 4: 406–425
- Sakai H, Medrano LJ, Meyerowitz EM (1995) Role of SUPERMAN in maintaining *Arabidopsis* floral whorl boundaries. **Nature** 378: 199–203
- Schellmann S, Schnittger A, Kirik V, Wada T, Okada K, Beermann A, Thumfahrt J, Jürgens G, Hülskamp M (2002) TRIPTYCHON and CAPRICE mediate lateral inhibition during trichome and root hair patterning in *Arabidopsis*. **EMBO J** 21: 5036–5046
- Schiefelbein J, Kwak S-H, Wieckowski Y, Barron C, Bruex A (2009) The gene regulatory network for root epidermal cell-type pattern formation in *Arabidopsis*. **J Exp Bot** 60: 1515–1521
- Sun L, Zhou Z, An L, Yan A, Zhao Y, Meng X, Steele-King C, Gan Y (2013) GLABROUS INFLORESCENCE STEMS regulates trichome branching by genetically interacting with SIM in *Arabidopsis*. **J Zhejiang Univ Sci B** 14: 563–569
- Sun S, Guo S, Yang X, Bao Y, Tang H, Sun H, Huang J, Zhang H (2010) Functional analysis of a novel Cys2/His2-type zinc finger protein involved in salt tolerance in rice. **J Exp Bot** 61: 2807–2818
- Szymanski DB, Lloyd AM, Marks MD (2000) Progress in the molecular genetic analysis of trichome initiation and morphogenesis in *Arabidopsis*. **Trends Plant Sci** 5: 214–219
- Takatsuji H (1998) Zinc-finger transcription factors in plants. **Cell Mol Life Sci** 54: 582–596
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood evolutionary distance, and maximum parsimony methods. **Mol Biol Evol** 28: 2731–2739
- Telfer A, Bollman KM, Poethig RS (1997) Phase change and the regulation of trichome distribution in *Arabidopsis thaliana*. **Development** 124: 645–654
- Tian Z, Zhang Y, Liu J, Xie C (2010) Novel potato C₂H₂-type zinc finger protein gene, StZFP1, which responds to biotic and abiotic stress, plays a role in salt tolerance. **Plant Biol** 12: 689–697
- Tominaga-Wada R, Ishida T, Wada T (2011) New insights into the mechanism of development of *Arabidopsis* root hairs and trichomes. In: Kwang WJ, ed. *International Review of Cell and Molecular Biology*. Academic Press, Amsterdam. pp. 67–106
- Wada T, Tachibana T, Shimura Y, Okada K (1997) Epidermal cell differentiation in *Arabidopsis* determined by a Myb homolog, CPC. **Science** 277: 1113–1116
- Walker AR, Davison PA, Bolognesi-Winfield AC, James CM, Srinivasan N, Blundell TL, Esch JJ, Marks MD, Gray JC (1999) The TRANSPARENT TESTA GLABRA1 locus, which regulates trichome differentiation and anthocyanin biosynthesis in *Arabidopsis*, encodes a WD40 repeat protein. **Plant Cell** 11: 1337–1349
- Wang Y, Dou D, Wang X, Li A, Sheng Y, Hua C, Cheng B, Chen X, Zheng X, Wang Y (2009) The PsCZF1 gene encoding a C₂H₂ zinc finger protein is required for growth, development and pathogenesis in *Phytophthora sojae*. **Microb Pathog** 47: 78–86
- Wang Y, Hou Y, Gu H, Kang D, Chen ZL, Liu J, Qu LJ (2013) The *Arabidopsis* anaphase-promoting complex/cyclosome subunit 1 is critical for both female gametogenesis and embryogenesis. **J Integr Plant Biol** 55: 64–74
- Wester K, Digiuni S, Geier F, Timmer J, Fleck C, Hülskamp M (2009) Functional diversity of R₃ single-repeat genes in trichome development. **Development** 136: 1487–1496
- Xiao H, Tang J, Li Y, Wang W, Li X, Jin L, Xie R, Luo H, Zhao X, Meng Z (2009) STAMENLESS 1, encoding a single C₂H₂ zinc finger protein, regulates floral organ identity in rice. **Plant J** 59: 789–801
- 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

- Yang C, Ye Z (2013) Trichomes as models for studying plant cell differentiation. **Cell Mol Life Sci** 70: 1937–1948
- Yun JY, Weigel D, Lee I (2002) Ectopic expression of *SUPERMAN* suppresses development of petals and stamens. **Plant Cell Physiol** 43: 52–57
- Zhang H, Ni L, Liu Y, Wang Y, Zhang A, Tan M, Jiang M (2012) The C2H2-type zinc finger protein ZFP182 is involved in abscisic acid-induced antioxidant defense in rice. **J Integr Plant Biol** 54: 500–510
- Zhao H, Li X, Ma L (2012) Basic helix-loop-helix transcription factors and epidermal cell fate determination in *Arabidopsis*. **Plant Signal Behav** 7: 1556–1560
- Zhao M, Morohashi K, Hatlestad G, Grotewold E, Lloyd A (2008) The TTG1-bHLH-MYB complex controls trichome cell fate and patterning through direct targeting of regulatory loci. **Development** 135: 1991–1999
- Zhou Z, An L, Sun L, Gan Y (2012) ZFP5 encodes a functionally equivalent GIS protein to control trichome initiation. **Plant Signal Behav** 7: 28–30
- Zhou Z, An L, Sun L, Zhu S, Xi W, Broun P, Yu H, Gan Y (2011) Zinc finger protein5 is required for the control of trichome initiation by acting upstream of Zinc finger protein8 in *Arabidopsis*. **Plant Physiol** 157: 673–682
- Zhou Z, Sun L, Zhao Y, An L, Yan A, Meng X, Gan Y (2013) Zinc Finger Protein 6 (ZFP6) regulates trichome initiation by integrating gibberellin and cytokinin signaling in *Arabidopsis thaliana*. **New Phytol** 198: 699–708