

Trichome Formation: Gibberellins on the Move

Plant trichomes are specialized epidermal protrusions that, depending on species, are located on the surfaces of leaves, stems, petioles, sepals, seed coats, and other aerial organs. Trichomes not only defend plants against biotic and environmental hazard, but also are able to synthesize, store, and secrete a large number of specialized (secondary) metabolites, including those with significant commercial value (Schillmiller et al., 2008). In addition, trichome formation is an excellent model to study cell fate specification and cell type patterning (Robinson and Roeder, 2015). The patterns of trichomes could be explained by cell-cell communication-based lateral inhibition of surrounding epidermal cells (Langdale, 1998). In *Arabidopsis*, a gene regulatory network controlling trichome formation and patterning has emerged, which includes an immobile activating protein complex and mobile inhibitors (Pattanaik et al., 2014). Trichome formation is promoted by the activating protein complex containing three groups of transcription factors: the R2R3 MYB, basic helix-loop-helix, and WD40 repeat proteins. The activating complex also activates the single repeat R3 MYB inhibitors, which can move to neighboring cells and repress trichome formation. In addition, phytohormones are involved in trichome formation, including GA as a promoter of trichome initiation (Chien and Sussex, 1996). Although phytohormones often are mobile signaling molecules, the distribution and transportation of GA have not been taken into account for trichome formation.

In this issue, Matías-Hernández et al. (2016) reported that two transcription factors, TEMPRANILLO1 (TEM1) and TEM2, inhibit trichome initiation from the underneath layer of the epidermis, the mesophyll. Matías-Hernández et al. (2016) found that *TEM* genes expressed in the mesophyll cells can still affect epidermal trichome formation, suggesting the existence of a non-cell-autonomous regulation. Surprisingly, bioactive fluorescently labeled GA₃, which was applied on top of leaves, accumulated exclusively in the mesophyll cells, but not in the epidermis, suggesting that the distribution of GA is under active regulation.

Recent studies have shown that GA movement and distribution are likely under regulation. In the root, GA distribution is endodermal specific and is likely an active and highly regulated process (Shani et al., 2013). Moreover, the NITRATE TRANSPORTER1/PEPTIDE TRANSPORTER FAMILY (NPF) proteins, originally identified as nitrate and peptide transporters, also can transport plant hormones, including auxin, abscisic acid, jasmonic acid, and GA, as well as specialized metabolites. GA transport activity has been confirmed

for a number of NPFs using an engineered yeast system (Chiba et al., 2015; Saito et al., 2015).

Indeed, TEMs suppress the expression of these newly identified GA transporters, and also suppress GA biosynthesis, to regulate GA distribution (Matías-Hernández et al., 2016). In fact, TEMs can reduce the mesophyll-specific accumulation of fluorescently labeled GA₃. Thus, TEMs regulate GA homeostasis in mesophyll cells to affect trichome formation in the epidermis. In addition, TEMs regulate signaling of cytokinin, a phytohormone that also promotes trichome formation.

Taken together, this new finding highlights the importance of GA transport and distribution in the regulation of trichome formation. Although the pivotal roles of auxin transport and distribution have gained enormous attention, relatively little is known about the transport and distribution of other phytohormones, which are also key regulators of development and environmental responses. This new study pointed out the importance of GA distribution in leaves, and one would expect more findings regarding the transportation of GA and other phytohormones in addition to auxin. It remains to be answered how mesophyll-accumulated GA affects epidermis cell fate specification. More detailed understanding of GA transportation kinetics and subcellular NPF protein localization would also shed new light on our understanding of GA distribution within plants.

Yuling Jiao*

State Key Laboratory of Plant Genomics,
Institute of Genetics and
Developmental Biology,
Chinese Academy of Sciences,
and National Center for Plant Gene Research,
Beijing 100101, China
ORCID IDs: 0000-0002-1189-1676 (Y.J.)

ACKNOWLEDGMENTS

I thank Luis Matías-Hernández and Soraya Pelaz for comments.

Received February 2, 2016; accepted February 3, 2016; published March 7, 2016.

LITERATURE CITED

- Chiba Y, Shimizu T, Miyakawa S, Kanno Y, Koshiba T, Kamiya Y, Seo M (2015) Identification of *Arabidopsis thaliana* NRT1/PTR FAMILY (NPF) proteins capable of transporting plant hormones. *J Plant Res* **128**: 679–686
- Chien JC, Sussex IM (1996) Differential regulation of trichome formation on the adaxial and abaxial leaf surfaces by gibberellins and photoperiod in *Arabidopsis thaliana* (L.) Heynh. *Plant Physiol* **111**: 1321–1328
- Langdale JA (1998) Cellular differentiation in the leaf. *Curr Opin Cell Biol* **10**: 734–738
- Matías-Hernández L, Aguilar-Jaramillo AE, Osnato M, Weinstain R, Shani E, Suárez-López P, Pelaz S (2016) TEMPRANILLO reveals the

* Address correspondence to yljiao@genetics.ac.cn.
www.plantphysiol.org/cgi/doi/10.1104/pp.16.00181

- mesophyll as crucial for epidermal trichome formation. *Plant Physiol* **170**: 1624–1639
- Pattanaik S, Patra B, Singh SK, Yuan L** (2014) An overview of the gene regulatory network controlling trichome development in the model plant, *Arabidopsis*. *Front Plant Sci* **5**: 259
- Robinson DO, Roeder AH** (2015) Themes and variations in cell type patterning in the plant epidermis. *Curr Opin Genet Dev* **32**: 55–65
- Saito H, Oikawa T, Hamamoto S, Ishimaru Y, Kanamori-Sato M, Sasaki-Sekimoto Y, Utsumi T, Chen J, Kanno Y, Masuda S, et al** (2015) The jasmonate-responsive GTR1 transporter is required for gibberellin-mediated stamen development in *Arabidopsis*. *Nat Commun* **6**: 6095
- Schilmiller AL, Last RL, Pichersky E** (2008) Harnessing plant trichome biochemistry for the production of useful compounds. *Plant J* **54**: 702–711
- Shani E, Weinstain R, Zhang Y, Castillejo C, Kaiserli E, Chory J, Tsien RY, Estelle M** (2013) Gibberellins accumulate in the elongating endodermal cells of *Arabidopsis* root. *Proc Natl Acad Sci USA* **110**: 4834–4839