Tissue-specific auxin signaling in response to temperature fluctuation

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Auxin levels are well regulated in cells and tissues by both transport and local biosynthesis, and its distribution is important for the modulation of cell proliferation, differentiation, development, tropisms and high-temperature response. Activation of auxin biosynthesis with increased temperatures reported in certain plant tissues. In contrast, our studies indicated that male tissue-specific auxin reduction via transcriptional repression of the *YUCCA* auxin biosynthesis genes is the primary cause of high temperature injury, which leads the abortion of pollen development in *Arabidopsis* and barley *Hordeum vulgare* L. Furthermore, the abortion can be reversed by the application of exogenous auxin, suggesting that the application may maintain crop yields during the current global warming crisis.

Key words: anther development, DR5-GUS, high temperature injury, male sterility, phytohormone

Abbreviations: GUS, β -glucuronidase; HT, high temperature; IAOx, indole-3-acetaldoxime; SAM, shoot apical meristem

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pin-formed phenotype.² PIN1 is a member of the PIN protein family, which provide directional auxin transport in response to various endogenous and environmental signals.³

Auxin IAA biosynthesis occurs mainly via a tryptophan-dependent pathway that includes four parallel and partially-interdependent pathways.^{5,6} The *YUCCA* (*YUC*) family of auxin synthetic genes encode flavin monooxygenases, which are involved in an pathway that produces IAA via the intermediate indole-3-acetaldoxime (IAOx).⁷ The *Arabidopsis YUC* family comprises 11 members and double, triple and quadruple mutant combinations display strong inflorescence and floral developmental defects, as well as alterations to leaf vasculature.⁸ The expression patterns of certain *YUCCA* genes are controlled spatially and temporally in developing anthers.^{8–10} Ikeda et al.¹¹ have indicated that in root tips, auxin biosynthesis occurs through expression of the anthranilate synthase, and it contributes to generation of a homeostatic gradient and local activation of auxin signaling. Thus, regulation of auxin levels in cells and tissues is achieved by both transport and local biosynthesis of auxin, and the distribution of auxin is important for transcriptional control of differentiation and development.^{1,12}

Although plants can grow over a broad range of temperatures, exposure to high temperatures (HT) results in dramatic changes to development, including rapid extension of plant axes, leaf hyponasty and early flowering.^{13,14} In *Arabidopsis*, HT promotes auxin-mediated elongation of hypocotyls.¹³ In hypocotyls, cotyledons and roots, HT-induced elongation requires upregulation of the tryptophan aminotransferase-encoding gene

Phytohormones are signaling molecules that regulate various aspects of plant growth, development, differentiation and adaptation. The phytohormone auxin is essential for the modulation of many processes including cell proliferation, development, phototropism, gravitropism, hydrotropism, apical dominance, senescence and cell specificity.¹ The shoot apical meristem (SAM) is responsible for generating all the aerial parts of a plant including the floral meristem, and auxin plays a key role in meristem activities. Regulation of the auxin distribution pattern in meristem tissues is performed by the auxin transporter families, PIN^{2,3} and AUX (auxin influx carrier),¹ as well as by local and tissue-specific auxin biosynthesis.⁴

Efflux carriers transport auxin from cell to cell in a polar manner. One such carrier, PIN1, was first identified in an *Arabidopsis* mutant that exhibited a

Figure 1. Temperature affects DR5-GUS expression in developing Arabidopsis anthers at stage 10. Flowering transgenic Arabidopsis DR5-GUS plants were cultured at 23°C and then transferred to growth cabinets at 10 or 31°C. After 24 h exposure to different temperatures, floral apices were dissected and stained for β -glucuronidase activity.

TAA1/TIR2A, which is involved in one of the auxin biosynthetic pathways.¹⁵⁻¹⁷ CYP79B2 and CYP79B3, Arabidopsis cytochrome P450s involved in pathways that synthesize auxin via IAOx, have also been shown to play roles in hypocotyl elongation.¹⁸ Recently, Koini et al.¹⁹ demonstrated that HT-induced architectural adaptations are mediated by the bHLH transcriptional regulator PIF4. Thus, PIF4-deficient mutants do not exhibit HT-induced elongation responses, leaf hyponasty or auxin-responsive gene *IAA29* upregulation. These results suggest that PIF4 responds to temperature signaling by interacting with the auxin response via biosynthesis.¹⁹

In some plant species, male reproduction is particularly susceptible to environmental stress and HT stress can cause significant injury during anther development.²⁰ Thus, the recent global warming trend represents a threat to plant reproduction processes. Lobell and Field²¹ have reported a negative correlation between increased temperatures and worldwide yields of wheat, maize and barley. They estimate that for these crops alone, global warming has resulted in an annual combined loss of approximately 40 megatons, or \$5 billion, per year since 1981.

HT increases auxin levels in many tissues.^{13,17-19} However, we demonstrated that HT upregulates expression of certain auxin-repressed proteins in barley panicles, which suggests that HT mediates depletion of auxin in reproductive tissues.²² In fact, HT conditions reduce endogenous auxin levels and auxin activity in the developing anthers of barley and Arabidopsis (Fig. 1).²³ Increasing temperatures also repress expression of Arabidopsis *YUC2*, *YUC6* and barley homologs.²³ Interestingly, the mutant phenotypes of

Arabidopsis double or triple mutants of *yuc2* and *yuc6*, are quite similar to the injuries observed in male reproductive development following HT stress. Specifically, these mutants completely lose male fertility and form short stamens that lack pollen grains.⁸ We observed that increased temperatures amplify auxin signals at the top of the gynoecium and around the vascular cells of petals in Arabidopsis (Fig. 1), as well as in rachis cells around the vascular bundles of developing barley panicles.²³ However, HT treatment clearly represses auxin signaling in an anther cell-specific manner, leading to abortion of pollen development and filament elongation. In both Arabidopsis and barley, the application of exogenous auxin can reverse abortion of pollen development and male sterility. Since a reduction in male tissue-specific auxin appears to be the primary result of HT injury in monocots and dicots, auxin treatment may be useful for promoting plant fertility and maintaining crop yields during the current global warming crisis.²³ Surprisingly, decreasing temperatures have the opposite effect on anther cells, which respond by increasing auxin signaling activities (Fig. 1). These findings lead to the conclusion that tissue-specific auxin signaling is a finely modulated response to temperature fluctuation, and that it is controlled using the auxin transport system and local biosynthesis.

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References

- Teale WD, Paponov IA, Palme K. Auxin in action: signalling, transport and the control of plant growth and development. *Nat Rev Mol Cell Biol* 2006; 7:847-59.
- Okada K, Ueda J, Komaki MK, Bell CJ, Shimura Y. Requirement of the auxin polar transport system in early stages of Arabidopsis floral bud formation. *Plant Cell* 1991; 3:677-84.
- Friml J. Subcellular trafficking of PIN auxin efflux carriers in auxin transport. *Eur J Cell Biol* 2010; 89:231-5.
- Vernoux T, Besnard F, Traas J. Auxin at the shoot apical meristem. *Cold Spring Harb Perspect Biol* 2010; 2:1487.
- Woodward AW, Bartel B. Auxin: Regulation, action and interaction. *Ann Bot* 2005; 95:707-35.
- Normanly J. Approaching cellular and molecular resolution of auxin biosynthesis and metabolism. *Cold Spring Harb Perspect Biol* 2010; 2:1594.
- Zhao Y, Christensen SK, Fankhauser C, Cashman JR, Cohen JD, Weigel D, et al. A role for flavin monooxygenase-like enzymes in auxin biosynthesis. *Science* 2001; 291:306-9.
- Cheng Y, Dai X, Zhao Y. Auxin biosynthesis by the YUCCA flavin monooxygenases controls the formation of floral organs and vascular tissues in Arabidopsis. *Genes Dev* 2006; 20:1790-9.
- Hirano K, Aya K, Hobo T, Sakakibara H, Kojima M, Shim RA, et al. Comprehensive transcriptome analysis of phytohormone biosynthesis and signaling genes in microspore/pollen and tapetum of rice. *Plant Cell Physiol* 2008; 49:1429-50.
- Cecchetti V, Altamura MM, Falasca G, Costantino P, Cardarelli M. Auxin regulates Arabidopsis anther dehiscence, pollen maturation and filament elongation. *Plant Cell* 2008; 20:1760-74.
- Ikeda Y, Men S, Fischer U, Stepanova AN, Alonso JM, Ljung K, et al. Local auxin biosynthesis modulates gradient-directed planar polarity in Arabidopsis. *Nat Cell Biol* 2009; 11:731-8.
- Kieffer M, Neve J, Kepinski S. Defining auxin response contexts in plant development. *Curr Opin Plant Biol* 2010; 13:12-20.
- Gray WM, Ostin A, Sandberg G, Romano CP, Estelle M. High temperature promotes auxin-mediated hypocotyl elongation in Arabidopsis. *Proc Natl Acad Sci USA* 1998; 95:7197-202.
- Balasubramanian S, Sureshkumar S, Lempe J, Weigel D. Potent induction of *Arabidopsis thaliana* flowering by elevated growth temperature. *PLoS Genet* 2006; 2:106.
- Stepanova AN, Robertson-Hoyt J, Yun J, Benavente LM, Xie DY, Dolezal K, et al. TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. *Cell* 2008; 133:177-91.
- Tao Y, Ferrer JL, Ljung K, Pojer F, Hong F, Long JA, et al. Rapid synthesis of auxin via a new tryptophan-dependent pathway is required for shade avoidance in plants. *Cell* 2008; 133:164-76.
- Yamada M, Greenham K, Prigge MJ, Jensen PJ, Estelle M. The *TRANSPORT INHIBITOR RESPONSE2* gene is required for auxin synthesis and diverse aspects of plant development. *Plant Physiol* 2009; 151:168-79.
- Zhao Y, Hull AK, Gupta NR, Goss KA, Alonso J, Ecker JR, et al. Trp-dependent auxin biosynthesis in Arabidopsis: involvement of cytochrome P450s CYP79B2 and CYP79B3. *Genes Dev* 2002; 16:3100-12.

19. Koini MA, Alvey L, Allen T, Tilley CA, Harberd NP, Whitelam GC, et al. High temperature-mediated adaptations in plant architecture require the bHLH transcription factor PIF4. *Curr Biol* 2009; 19:408-13.
20. Sakata T, Higashitani A. Male sterility accompanied with abnormal anther development in plants—Genes and environmental stresses with special reference to high temperature injury. *Intl J Plant Dev Biol* 2008; 2:42-51.
21. Lobell DB, Field CB. Global scale climate-crop yield relationships and the impacts of recent warming. *Environ Res Lett* 2007; 2:14002.
22. Oshino T, Abiko M, Saito R, Ichiishi E, Endo M, Kawagishi-Kobayashi M, et al. Premature progression of anther early developmental programs accompanied by comprehensive alterations in transcription during high-temperature injury in barley plants. *Mol Genet Genom* 2007; 278:31-42.
23. Sakata T, Oshino T, Miura S, Tomabeche M, Tsunaga Y, Higashitani N, et al. Auxins reverse plant male sterility caused by high temperatures. *Proc Natl Acad Sci USA* 2010; 107:8569-74.