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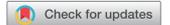


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SHORT COMMUNICATION



External coincidence model for hypocotyl thermomorphogenesis

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ABSTRACT

High but nonstressful temperatures profoundly affect plant growth and developmental processes, termed thermomorphogenesis. Thermo-induced hypocotyl elongation is a typical thermomorphogenic trait, which contributes to cooling plant organs. It is known that external light signals and the circadian clock coordinate rhythmic hypocotyl growth. However, it was unclear how light, temperature, and circadian rhythms are harmonized during hypocotyl thermomorphogenesis. We have recently demonstrated that the E3 ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) is activated at warm temperatures. It is notable that warm temperatures induce the nuclear import of COP1, facilitating degradation of ELONGATED HYPOCOTYL 5 (HY5) and this biochemical event is uncoupled from light conditions. Furthermore, the thermo-induced HY5 protein turnover occurs independent of circadian rhythms, indicating that the COP1-HY5 module conveys warm temperature information. Meanwhile, the clock components, including CIRCADIAN CLOCK ASSOCIATED 1 (CCA1), convey timing information for the rhythmic thermomorphogenic growth. These molecular mechanisms enable a coincidence between warm temperature signaling and circadian rhythms, which explains the distinct rhythms of hypocotyl growth at warm temperatures.

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Circadian clock; COP1; HY5; hypocotyl growth; thermomorphogenesis

Global warming is a worldwide issue in recent years, which imposes dramatic impacts on the Earth's ecosystem.¹ Plants are highly sensitive to even mild changes in ambient temperatures. It is widely perceived that plants actively modulate their architecture to optimize their growth and development under fluctuating temperature conditions.² Hypocotyls and leaf petioles are elongated, leaves are elevated, and flowering time is accelerated in response to warm temperatures.³ It has been reported that plant thermomorphogenesis is required for plant cooling capacity, which protects plant organs from heat damages.⁴

It is well-known that hypocotyl elongation is regulated by both internal and external cues.⁵ Light is one of the major environmental signals that mediate hypocotyl growth. During the daytime, light-activated phytochromes functionally suppress the basic helix-loop-helix transcription factors PHYTOCHROME INTERACTING FACTORS (PIFs).⁶ In the early evening, the circadian clock component EARLY FLOWERING 3 represses the expression of the PIF transcription factor genes.⁷ It is known that hypocotyl elongation occurs mainly during the late night, when PIF transcription factors are stabilized.⁵ However, how temperature signals are integrated with light information and circadian rhythms remained mostly elusive.

We have recently demonstrated that hypocotyl thermomorphogenesis is uncoupled from light periods.⁸ It has been observed that while Col-0 seedlings exhibited thermo-induced hypocotyl elongation under both light and dark conditions,

hypocotyl elongation was insensitive to warm temperatures in the COP1-defective *cop1-4* mutants. PIF4 and the auxin biosynthetic enzyme YUCCA8 (YUC8) are required for hypocotyl thermomorphogenesis.⁹ Notably, thermal induction of PIF4 and YUC8 genes was impaired in *cop1-4* mutants under both light and dark conditions, suggesting that COP1-mediated thermal responses of hypocotyl growth is independent of light.

The basic leucine zipper transcription factor HY5, which is a well-known substrate of COP1, is known to mediate plant thermomorphogenesis.¹⁰ We have shown that the expressions of PIF4 and several PIF4 target genes, including YUC8, ARABIDOPSIS THALIANA HOMEODOMAIN PROTEIN 2, and SMALL AUXIN UP RNA 24,^{11,12} were elevated in the *hy5-221* mutants (Fig. 1). It has also been shown that HY5 is degraded at warm temperatures under both light and dark conditions and the increased turnover of HY5 protein at warm temperatures depends is mediated by COP1. It is therefore evident that the COP1-HY5 module perceives warm temperature signals independent of light.

A critical question is how COP1 regulates HY5 abundance at warm temperature. Gene expression and protein abundance of COP1 are not affected by warm temperatures. It has been reported that the nuclear import of COP1 is regulated by various environmental signals.^{13,14} Interestingly, the nuclear import of COP1 is enhanced at 28°C. These observations indicate that thermal activation of COP1 is responsible for the temperature-dependent fluctuations in HY5 abundance.

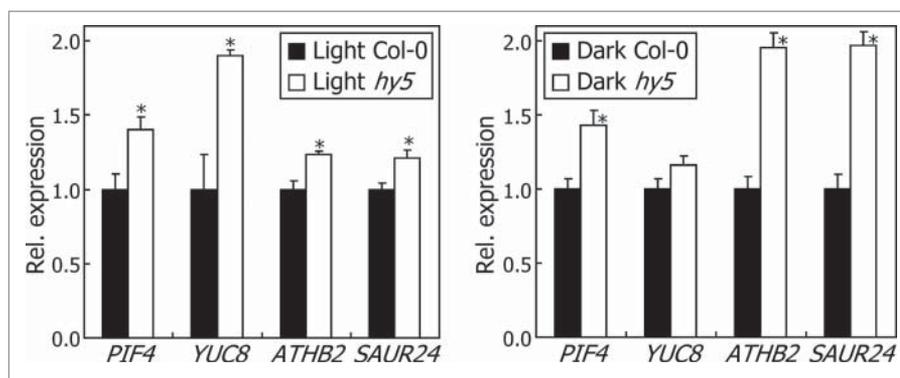


Figure 1. Expression of growth-promoting genes in *hy5-221* mutant. Seedlings were grown at 23°C under constant light conditions for 5 d and further grown at either 23°C or 28°C for 1 additional day under either constant light (left panel) or dark conditions (right panel). Transcript levels were examined by reverse transcription-mediated quantitative real-time PCR. Biological triplicates were statistically analyzed using Student *t*-test (**P* < 0.01). Bars indicate standard error of the mean.

Kinetic measurements of Col-0 seedling growth at 28°C have shown that thermo-induced hypocotyl elongation occurs at the specific time period during the day.⁸ Meanwhile, HY5 degradation at 28°C still occurs independent of circadian rhythms, suggesting that the COP1-HY5 module acts in temperature signaling but does not determine when to initiate hypocotyl thermomorphogenesis. We have shown that the circadian clock conveys timing information into hypocotyl thermomorphogenesis. The 35S:CCA1 seedlings still showed hypocotyl thermomorphogenesis, but they exhibited arrhythmic growth patterns. These results are consistent with a recent report that one of circadian clock components TIMING OF CAB EXPRESSION 1 is required for the circadian gating of hypocotyl thermomorphogenesis.¹⁵ It is now clear that circadian rhythms are important for the timing control of thermomorphogenic hypocotyl growth.

On the basis of the previous and our own data, we propose a coincidence model for hypocotyl thermomorphogenesis. The COP1-HY5 module conveys warm temperature information. Meanwhile, the circadian rhythms conveys timing information. Integration of the 2 signals mediates the circadian gating of hypocotyl thermomorphogenesis, leading to distinct patterns of hypocotyl growth at warm temperatures (Fig. 2).

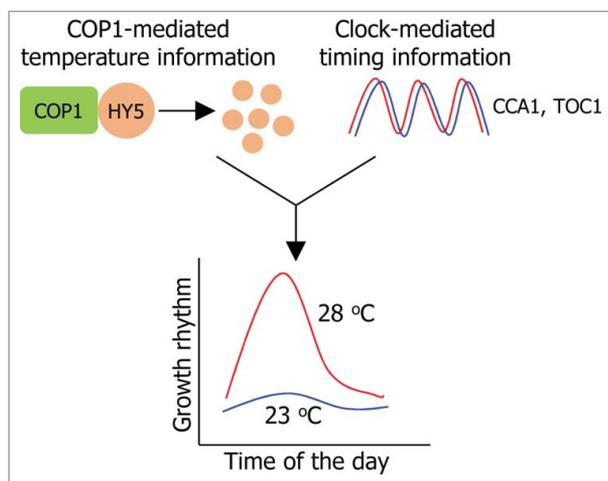


Figure 2. A schematic coincidence model for hypocotyl thermomorphogenesis. The COP1-HY5 module monitors warm temperature information. Meanwhile, the circadian clock conveys timing information. Hypocotyl thermomorphogenic growth occurs only when the COP1-HY5 module is thermally activated at the clock-gated time points.

A remaining question is how COP1 is thermally activated. Recent studies have shown that the red and far-red photoreceptors phytochromes function as thermosensors.^{16,17} Notably, the amount of the Pfr form is decreased in response to warm temperatures.¹⁷ Furthermore, it has been reported that the phytochromes inhibit the nuclear localization of COP1 under red-light conditions.¹⁸ Thus, it is likely that the thermo-induced Pfr-to-Pr conversion of the phytochrome photoreceptors is closely associated with the thermal activation of COP1. The potential linkage between the phytochrome photoreceptors and COP1 would enhance our understanding of signaling crosstalks between light and temperature signals.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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