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SHORT COMMUNICATION

Light priming of thermotolerance development in plants

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ABSTRACT

It is widely perceived that plant responses to environmental temperatures are profoundly influenced by light conditions. However, it is unknown how light signals modulate plant thermal responses and what photoreceptors are responsible for the light regulation of thermal adaptive process. We have recently reported that phytochrome B (phyB)-mediated red light signals prime the ASCORBATE PEROXIDASE 2 (APX2)-mediated detoxification reaction of reactive oxygen species (ROS), a well-known biochemical process that mediates the acquisition of thermotolerance under high temperature conditions. It is interesting that red light influences the HEAT SHOCK FACTOR A1 (HSFA1)-stimulated activation of the *APX2* transcription, which is otherwise responsive primarily to stressful high temperatures. Blue light also efficiently primes the APX2-mediated induction of thermotolerance. In natural habitats, temperatures fluctuate according to the light/dark cycles with temperature peaks occurring during the daytime. It is thus apparent that plants utilize light information to prepare for upcoming high temperature spells.

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Text

Plant growth and developmental processes are profoundly affected by fluctuations in light and temperature conditions. In temperate regions, abrupt spells of high or cold temperatures frequently impose damaging effects on crop agriculture. In particular, there is a growing concern on global warming, a steady increase of average global temperature, in recent decades[1]. Therefore, it is evident that understanding molecular and physiological mechanisms directing the establishment of thermotolerance is a key to developing heat-resistant crops.

Plants have evolved diverse defense mechanisms to cope with high temperature stress,[2] among which the heat-induced detoxification of reactive oxygen species (ROS) has been most extensively studied.[3,4] Under high temperature conditions, plants triggers diverse ROS detoxification pathways to protect biological molecules from oxidative damages. The best characterized is the reduction of ROS accumulation by ASCORBATE PEROXIDASE (APX) enzymes that are functional under various stress conditions.[4] Notably, it is known that the APX2 enzyme functions primarily under heat stress conditions.[3]

There are numerous examples that illustrate the effects of light on the development of plant adaptation responses to both biotic and abiotic stresses. It is known that pathogen-induced expression of *PATHOGENESIS-RELATED* (*PR*) genes requires light illumination, and induction of disease resistance is more prominent in the light.[5] Similarly, it has been reported that plants grown under short days develop stronger freezing tolerance than those grown under long days,[6] emphasizing the co-occurrence of cold temperatures and short daylengths in nature. Interestingly, plant warm temperature responses are tightly linked with light sensing and signaling: multiple light signaling components also act as signaling mediators of warm temperature-induced hypocotyl elongation.[7–9] A seminal effect of light on the induction of stress resistance responses is its priming capability. Constitutive induction of stress resistance responses is harmful to plant growth and survival by causing growth retardation and architectural distortions.[10] Therefore, under optimal conditions, plants do not elicit stress-resistant responses but instead prepare for potentially upcoming environmental fluctuations at the molecular and physiological levels, which is often termed priming.[11,12] A well-characterized is the priming of defensive mechanisms in response to initial pathogen attacks in order to prepare for the future pathogen attacks.[13,14]

A recent report describes an example for light-mediated priming of stress-tolerant responses in plants. It has been shown that phyB-mediated red light priming of the ROS detoxification reaction is a critical biochemical event for the induction of thermotolerance development[3]. While thermotolerance responses were severely reduced at the end of the dark period, they were greatly enhanced during and right after the light period, indicating that light preincubation is required for the efficient induction of thermotolerance. ROS accumulate upon exposure to high temperatures, causing oxidative damages on biological molecules and structures, such as nucleic acids, proteins, and membranes,[3] entailing that their detoxification is a prerequisite for the induction of thermotolerance. It has been found that while ROS accumulate to a relative lower level in light-preincubated plants, their accumulation was much higher in plants incubated in the dark.

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Accordingly, exogenous application of the anti-oxidant ascorbate significantly enhanced the thermotolerance of dark-incubated seedlings, demonstrating that light primes the development of thermotolerance. A question is how light primes the thermotolerant responses.

Plants possess several ROS detoxification pathways to deal with the oxidative damages imposed by ROS accumulation,[15] among which the roles of APX enzymes have been extensively studied. APX enzymes convert hydrogen peroxide to water using ascorbate as substrate[4]. Notably, it has been reported that the APX enzyme activity is greatly elevated in light-preincubated plants.[16] We also found that the thermal induction of *APX2* transcription is more pronounced in light-grown plants.[16] The HSFA1 transcription factors directly activate the *APX* genes.[17] Consistent with the previous reports, we found that light priming of *APX2* transcription and the ROS detoxifying capacity of its protein product were abolished in Arabidopsis mutants lacking HSFA1-a, HSFA1-b, HSFA1-c, and HSFA1-d members, indicating that the HSFA1 transcription factors play a role in the light priming of thermotolerance.

A critical question is how light information is incorporated into the APX2-mediated thermotolerance pathway and which photoreceptors are responsible for the light priming event. An extensive set of thermotolerance assays has shown that red and blue lights were most efficient in priming the induction of thermotolerance. In addition, the light priming effects were diminished in phyB-defective mutants, indicating that phyB is responsible for the red light-mediated priming event. Blue light wavelength was also effective in priming plant responses to high temperatures. However, it is currently unclear which blue light receptors are involved in the light priming process.

Our data demonstrate that phyB-mediated red light priming targets the expression of *APX2* gene, possibly by modulating the functional mechanism of HSFA1 transcription factors (Figure 1). Possible working mechanisms would include light-triggered alterations of *APX* loci for efficient binding of HSFA1 transcription factors, modulation of their subcellular localization, or modification of their transcriptional activity. Alternatively, light signaling would stimulate as-yet unidentified factor, which facilitate the binding of HSFA1 transcription factors to the *APX2* promoter.

In nature, light and temperature fluctuate through mutually overlapped diurnal cycles: temperatures are usually lower in the dark but higher in the light. Therefore, it is not surprising that plants take advantage of light information to anticipate upcoming temperature events. It is interesting that most of the previous studies on photomorphogenesis have described light signaling as a modulator of transcriptional cascades,[18] our observations suggest that light priming of thermotolerance development might be associated with epigenetic regulation. Consistently, it has been reported that chromatin modification reactions are involved in acquired thermotolerance.[19] It will be interesting to investigate what chromatin modifiers are involved in the phyB-mediated red light priming of the HSFA1-controlled transcription of *APX2* gene.

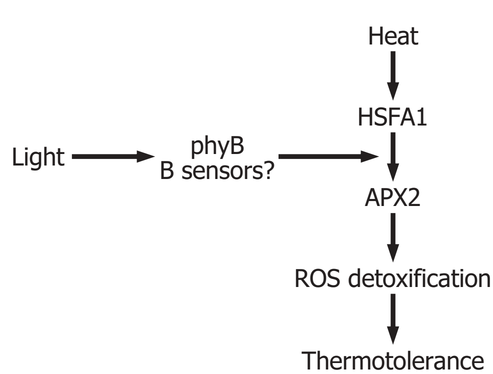

Figure 1. Light primes the induction of thermotolerance under heat stress conditions. Phytochrome B-sensed red light vitalizes the thermo-induced expression of *APX2* gene, whose protein product detoxifies ROS, finally resulting in the development of thermotolerance. Blue light (B) also primes the temperature-resistant response, while it is currently unclear which B receptor is responsible for the B-mediated priming process.

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Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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