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REVIEW

Priming: A promising strategy for crop production in response to future climate

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Abstract

Anticipated more frequent extreme events due to changes in global climatic variability requires adaptation of crop species to multi-occurrence abiotic stresses hereby sustaining the food security. Priming, by pre-exposure of plants to an eliciting factor, enables plants to be more tolerant to later biotic or abiotic stress events. Priming induced "stress memory" exists in both present generation and the offspring. Thus, priming is suggested to be a promising strategy for plants to cope with the abiotic stresses under global change scenarios. In this review, the underlying physiological and molecular mechanisms of priming induced enhancement of stress tolerance to the major abiotic stresses of drought and waterlogging, and high and low temperature in crop plants were discussed, and the potential to utilize the priming effect for sustaining crop productivity in future climates was also suggested.

Keywords: priming, stress memory, transgenerational priming, physiological mechanisms

1. Introduction

Compared to 1850–1900, the global mean temperature has increased 1.5–2.0°C by the end of the 21st century according to the latest report of the Intergovernmental Panel on Climate Change (Field *et al*. 2014). Following the increase in mean temperature, the frequency of extreme adversity events, such as episodes of extreme hot and cold temperatures, large changes in precipitation patterns, is predicted to increase dramatically (Piao *et al*. 2010; Fischer and Knutti 2015). Abiotic stresses such as heat, cold, drought, and flooding are now the major constraints for crop production which could cause great loss of crop yield (Deryng *et al*. 2014; Loreti *et al*. 2016). Thus, adaptation strategies are required to improve tolerance to the stresses, especially those occurring during the reproductive growth stages in order to sustain crop yield under more variable climates in the future.

Different strategies could improve plant tolerance to abiotic stress, but some of them are time-consuming (e.g., conventional breeding) (Antoniou *et al*. 2016), and some are species- and dose-dependent (e.g., exogenous application plant hormones), and a deeper understanding of the underlying mechanisms is needed. Priming, defined as pre-exposure of plants to an eliciting factor, could trigger crop "stress memory" enabling plants be better prepared

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to respond to later stress events. Priming has been considered as a cost-efficient strategy to improve plant tolerance to stress and has attracted intensive research recently (Bruce *et al*. 2007; Luna *et al*. 2012; Avramova 2015; Balmer *et al*. 2015; Kim *et al*. 2015; Vriet *et al*. 2015; Martinez-Medina *et al*. 2016). Chemical priming is known to be able to enhance plant stress tolerance, and its underlying mechanisms have been well documented by Antoniou *et al*. (2016), and will not be included in this review. Priming stimulus comprises both biotic and abiotic categories, and the primed state includes post-challenge primed state in the same generation and the stress memory passing down to the next generation, i.e., the transgenerational primed state. Changes in hormones, metabolites, sugar signals, reactive oxygen species (ROS), and other signals are induced by priming which enhance tolerance of the plants to the succeeding stressors (Fig. 1). Compared with the non-primed plants, the primed plants by pathogens or beneficial microbes showed faster or stronger defense responses against subsequent biotic or abiotic stress in the same generation (Conrath 2011). Biotically induced priming mechanisms including the regulation of primary metabolism, an increase in the levels of pattern-recognition receptors, an accumulation of mitogen-activated protein kinases, and chromatin modification, etc., have been comprehensively reviewed (Slaughter *et al*. 2012; Balmer *et al*. 2015; Conrath *et al*. 2015). It has also been demonstrated that the biotic stresses (disease, pathogen, etc.) induced priming could be inherited epigenetically to protect their progeny against recurred biotic stress without permanent genetic fixation of the trait in *Arabidopsis* (Luna *et al*. 2012). Abiotic stress induced priming has also attracted more and more attention (Boyko and Kovalchuk 2011; Mirouze and Paszkowski 2011), since both post-challenge primed memory and transgenerational memory in plants could be adopted as active strategies to cope with adverse environmental perturbations. Mirouze and Paszkowski (2011) summarized that the epigenetic regulation contributes to plant stress adaptation. Boyko and Kovalchuk (2011) reviewed the evidence for transgenerational hardening, and discussed the recent advances in genome instability and epigenetically mediated plant transgenerational adaptation. However, the physiological basis of abiotic stress induced priming is still unclear and merits further investigations.

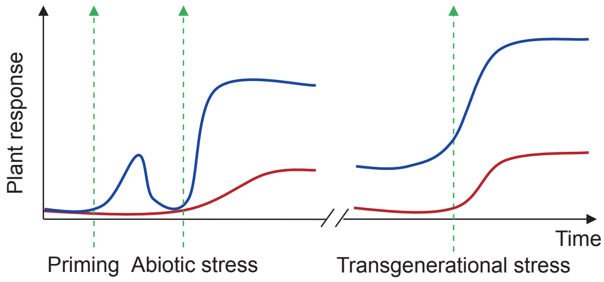

Fig. 1 Scheme of the plant priming responses in the same generation and transgeneration. The reaction level is shown in primed plants (blue) or un-primed plants (red) under different states of priming. Adapted from Balmer *et al.* (2015).

In this paper, we highlight the state-of-the-art of physiological and biological mechanisms involved in the abiotic stress priming, including both post-challenge primed state and transgenerational primed state.

2. Post-challenge primed state

2.1. Heat priming defends against heat stress

During reproductive growth stages of plants, particularly in cereals, temperatures higher than the optimum level could result in shorter grain filling period and cause great loss of grain yield (Hossain *et al*. 2015). Heat stress could occur at various stages of plant growth and development. Many critical physiological processes, such as photosynthesis, cell membrane stability, RNA splicing, and protein synthesis, are essentially affected by heat stress. The tolerance to heat stress depends on the ability of plants to perceive the stimulus, signalling transduction, physiological and biochemical adjustment (Hasanuzzaman *et al*. 2013). It has been confirmed that heat priming could effectively improve thermo-tolerance to the later recurred heat stress in several plant species (Wang *et al*. 2014; Zhang *et al*. 2016). In wheat, heat priming applied at the seven- and nine-leaf stages, with a day/night temperature of 32/28°C (increased 8°C compared with control) for two days, enhanced tolerance to heat stress occurring after anthesis. Under post-anthesis high temperature stress, in relation to the non-primed plants, heat primed plants showed higher photosynthetic capacity and enhanced ROS scavenging capacity, as indicated by higher photosynthetic rate, higher activities of superoxide dismutase (SOD) in chloroplasts as well as of glutathione reductase (GR) and peroxidase in mitochondria, which contributed to the lower cell membrane damage as indicated by lower malondialdehyde (MDA) content in chloroplasts and mitochondria of wheat leaf. The improved photosynthetic rate and antioxidant capacity were attributed to the up-regulated gene expressions of *Rab*, *Cu/Zn-SOD*, *Mn-SOD*, and *GR* in primed plants (Wang *et al*. 2011, 2013). In addition, compared with the non-primed plants, the primed plants possessed greater grain starch accumulation by enhancing reserve remobilization from vegetative organs to grains under post-anthesis high temperature, suggesting a maintenance of grain quality in the primed plants (Wang *et al*. 2012).

It is known that heat shock proteins (HSPs) are