Stress Memories for Better Tolerance in Plants—A Potential Strategy for Crop Breeding

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1. Introduction

Extreme weather events such as severe drought, high temperature, and waterlogging are important barriers limiting crop growth and productivity [1]. Climate change scenarios predict that the global average temperature will increase by 3.7–4.8 °C by 2100 and the distribution of precipitation will be hugely imbalanced, subjecting crops to multi-occurrences of abiotic stresses, which seriously restrict crop yield and quality [2]. Previous studies reported that global wheat and maize production have been reduced by 20.6 and 39.3% due to water deficiency [3]. Global crop production will be reduced by more than 10% by the middle of the 21st century due to warming temperatures [4]. Although this multi-occurrence of stresses may result in a detrimental effect on crops, an earlier stress event could provide a chance to prime plants to protect themselves against later stress [5]. The trigger for subsequent stress tolerance (i.e., the early moderate stress event) is referred to as priming. Priming-induced stress memory involves multiple modifications at physiological and biochemical processes in plants, e.g., antioxidant enzyme activities, osmotic regulation substances, signaling transduction pathways, and secondary metabolites, which help the plants to respond more quickly and effectively to recurrent stress or transmit this feasible protective measure to the next generation [6]. Therefore, giving priority to the signal communication and molecular mechanisms of plant stress memory and tolerance induction can provide novel insight into stress-resistant crop breeding and genetic improvement.

2. Priming and Stress Memory

Priming can elicit stress memory and thereby enhance the stress tolerance of plants. Stress memory involves multiple modifications at the physiological, proteomic, transcriptional levels and of the epigenetic mechanisms in plants [7]. Previous studies documented that single or double drought priming before anthesis results in a higher grain yield in wheat under drought stress occurring during grain filling [8]. The drought-primed plants possess a better leaf water status and higher photosynthesis rate and antioxidant capacity than the non-primed plants [8]. An up-regulated expression of proteins involved in photosynthesis and stress defense in primed plants contributes to the priming effects, enabling plants such as wheat to cope with drought [8]. Furthermore, drought priming in parental plants significantly improves heat tolerance in offspring wheat, which is related to a higher osmotic regulation capacity of the offspring to maintain a relatively balanced water potential in cells [9]. In addition, drought priming applied during stem elongation improves the heat tolerance of wheat during grain filling, as exemplified by lower energy dissipation and relatively higher CO2 assimilation in primed plants [10]. Also, the adverse impact
of low temperature is shown to be alleviated in plants primed with moderate drought compared to non-primed ones [11]. With a similar mechanism, radio-priming agents, such as He-Ne lasers, effectively reduce the levels of reactive oxygen species (ROS) by enhancing the activities of ascorbate peroxidase, peroxidase, superoxide dismutase, and catalase, thus protecting photosynthetic pigments, metabolic functions, and subcellular organs from oxidative damage and maintaining the normal physiological process and growth in wheat under drought [12]. This may also be related to the expressions of drought response genes [2]. In a transgenerational priming study, heat priming up-regulated the expression of the gene encoding lysine-specific histone demethylase 1 in offspring wheat, indicating that the transgenerational heat stress “memory” may be induced by epigenetic changes and signal transduction, thereby triggering the defense system [13]. Several genes related to drought stress “memory” are identified through specific sequencing of the transcriptome after repeated drought and rehydration treatments in rice [14]. Generally, priming can induce the modifications of major protein kinases through secondary signaling substances, such as abscisic acid (ABA), hydrogen peroxide (H$_2$O$_2$), and calcium ion (Ca$^{2+}$), to regulate stress response gene expressions, in turn enhancing plant stress memory and tolerance to subsequent stress [15].

3. Roles of ABA and Melatonin in Stress Tolerance

Phytohormones, such as ABA and melatonin, are involved in the regulation of plant stress response and play key roles in stress memory [16,17]. It is well known that ABA-based root-to-shoot chemical signaling can regulate seed germination and dormancy, root growth, leaf senescence, and stomatal movement, as well as the expression and transcription of stress response genes, hence improving plant abiotic stress adaptation [18]. The core components and signaling pathways of ABA biosynthesis in *Arabidopsis*, maize, cowpea, wheat, and bean under drought stress are closely related to the up-regulated expression of 9-cis-epoxycartenoid dioxygenase (NCED), which can increase the levels of ABA in plants, thereby regulating drought responses [19]. In addition, ABA is a dominant player in mediating the adaptation of plants to other abiotic stresses by improving their oxygen scavenging efficiency and increasing their sugar accumulation [20]. As a phytohormone and antioxidant, melatonin (N-acetyl-5-methoxytryptamine) is also involved in the signaling network in response to abiotic stress [21]. For instance, melatonin down-regulates *MdNCED3*, an ABA synthesis gene, while it up-regulates its catabolic genes, *MdCYP707A1* and *MdCYP707A2*, thereby reducing ABA concentration in drought-stressed plants [22]. At the physiological level, melatonin is involved in various processes, such as adjusting the oxygen scavenging system and carbon metabolism enzyme system in plants (Figure 1) [23,24].
Figure 1. Roles of melatonin in stress memory and crop tolerance induction. RWC, relative water content of leaf; $\psi_{\text{leaf}}$, leaf water potential; ABA, abscisic acid; $A_n$, net photosynthetic rate; $g_s$, stomatal conductance; $T_r$, transpiration rate; $F_v/F_m$, maximal photochemical efficiency; ROS, reactive oxygen species; POD, peroxidase; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; AsA, ascorbic acid; GSH, reduced glutathione; MDA, malondialdehyde.

4. Crop Breeding for Environmental Adaptability

Various strategies have been established for improving crop breeding to enhance performance and tolerance to climate change. The question of how to improve the environmental adaptability of crops is of importance for dealing with drier and warmer climates in the future. Stress memory, as a natural ability in plants, could be considered in the application of crop genetic improvement. The genes and pathways related to stress memory, especially the interaction of phytohormones, should be targeted as the potential genetic loci for germplasm selection. In addition, the transgenerational effects of stress memory should also be a key point in crop breeding, though they are most likely to be related to the epigenetic mechanism. Stress priming applied in parental plants may be a shortcut to producing stress-resistant offspring, which could be a novel approach to crop breeding.

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