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The landscape of molecular mechanisms for salt tolerance in wheat☆

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ABSTRACT

Wheat is one of the most important food crops, and its yield is seriously restricted by high salinity and other abiotic stresses. Many attempts have been made to elucidate the major physiological processes associated with salt tolerance and to identify the genes controlling the processes. In this review, the major role of high-affinity potassium transporter (HKT) genes in enhancing the salt tolerance of wheat is summarized. The link between maintenance of reactive oxygen species (ROS) homeostasis and salt tolerance through a comprehensive study of a wheat introgression line is examined, and the contribution of a set of genes involved in this process is depicted. New research strategies to uncover the mechanisms underlying salt tolerance in wheat based on recent advances in omics will be discussed.

Contents

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1. Introduction

Bread wheat (*Triticum aestivum* L.), one of the most important staple crops globally, provides most of the calories for approximately 30% of the world population [1]. Increasing attention is being given to the mechanisms of abiotic stress response due to greater awareness of the threats of climate change, and loss of arable land during urbanization, and environmental degradation caused by pollution [2]. Since more than 800 Mha (6%) of arable land are affected by salinity worldwide [3], soil salinity is a major constraint upon wheat grain yield [4].

A direct consequence of soil salinity is the over-accumulation of intracellular sodium (Na^+), resulting in serious ionic toxicity, especially in the leaves with direct inhibitory effects on photosynthesis. Moreover, salt stress can cause osmotic and oxidative stress, further disturbing metabolic processes and leading to DNA damage and even cell death [3]. Therefore, understanding the mechanisms of response and adaptation to salt stress and then improving the salinity tolerance of crops are critical tasks for breeders and researchers.

Although some mechanisms, such as osmotic adjustment, tissue tolerance processes, and K^+ retention, have been elaborated in other crops [5], these are greater challenges for bread wheat due to its large, complicated and hexaploid genome [6]. Nevertheless, the mechanisms underlying salinity tolerance in wheat, including leaf Na^+ exclusion mediated by high-affinity K^+ transporters (HKTs) and reactive oxygen species (ROS) detoxification, have been addressed in long-term and subtle ways [5]. Multiple components involved in crosstalk of salinity response with other environmental or developmental signals were identified. Notably, in line with the continuous releases of wheat whole genome information [7] and recently established wheat mutant libraries [8], more versatile approaches will be available for salt tolerance improvement. Therefore, this review will provide an outline of the mechanisms of wheat salinity tolerance, and present an outlook on prospective key research on this topic.

2. *HKT*-type transporters confer wheat salinity tolerance by promoting sodium exclusion

It has long been known that tetraploid wheat is less salt tolerant than bread wheat [9,10], and that a major factor behind this difference is that bread wheat is able to maintain a higher ratio of potassium concentration to sodium concentration in the leaves [11]. This trait was shown to be governed by *Kna1* on chromosome 4D [12]. A genetic analysis, based on a population derived from a cross between a standard durum wheat genotype and a line containing introgressions from the A genome diploid ancestral wheat relative *Triticum monococcum* showing high Na^+ exclusion ability, revealed that two loci, *Nax1* and *Nax2*, were involved in excluding sodium ions [13].

Class 1 *HKT* genes are involved in regulating transport of Na^+ in higher plants [14]. Several *HKT1* genes, including *HKT1;1/2*-like, *HKT1;3*-like, *HKT1;4*-like, and *HKT1;5*-like, have been identified and mapped to wheat homoeologous chromosome groups 2, 6, 2, and 4, respectively [15]. Among these, *Nax1* in chromosome arm 2AL co-segregated with sodium transporter gene *HKT1;4-A2*, which was shown to control Na^+ unloading from xylem in roots and sheaths and therefore was proposed as the functional candidate [16]. *Nax2* was mapped to the distal region of chromosome 5AL that is homoeologous to a region on chromosome 4DL containing *Kna1*. Based on synteny and phylogeny analysis with *Nax2*, *TmHKT1;5-A* was proposed to be the candidate of *Nax2* [17]. In addition, field trials in saline soils demonstrated that the presence of *TmHKT1;5-A* significantly reduced leaf sodium content and increased durum wheat grain yield by 25% compared to lines without the *Nax2* locus [18]. Furthermore, decreased expression of *TaHKT1;5-D*, which is homoeologous to *TmHKT1;5-A* and underlies *Kna1* locus in bread wheat, caused by target-specific RNA interference-induced silencing (RNAi), led to an accumulation of Na^+ in leaves [19], strongly suggesting that *TaHKT1;5-D* should be the candidate gene of *Kna1*.

Na^+ exclusion mediated by *HKT* genes in leaves has been recognized as a major mechanism in salinity tolerance of wheat. However, some fundamental issues need to be further addressed. One is how these *HKT* genes respond to salt stress in wheat. For example, *TaHKT1;5-D* exhibited a transcriptional reprogramming from constitutive high basal expression in diploid *Aegilops tauschii* to salt-induced expression in a newly synthetic allohexaploid wheat [20], whilst Byrt et al. [19] discovered no detectable difference in *TaHKT1;5-D* expression when hexaploid wheat cv. Bobwhite was challenged by salt stress. Additionally, a reduction in *TaHKT1;5-D* transcripts was revealed after salt treatment in both hexaploid wheat cv. JN177 and its introgression line SR3 [21]. These contradictory results bring about an interesting question of whether the response of *TaHKT1;5-D* to salinity is accession-dependent (that is, is there an association between the response mode and tolerance to salt stress?), or tissue-specific (as *TaHKT1;5-D* was previously implied to be predominantly functional within the stele, particularly within xylem parenchyma and pericycle cells adjacent to the xylem vessels [19]).

Another question is how these wheat *HKT* genes are regulated. The sole *HKT* gene in *Arabidopsis*, *AtHKT1*, is regulated by small RNA and DNA methylation [22]. Moreover, DNA methylation also participated in the response of *TaHKT1;5s* to salt stress in wheat cv. JN177 and SR3 [21]. Intriguingly, the transcript levels of *TaHKT1;5-B1* and *TaHKT1;5-B2* were extremely low compared with that of *TaHKT1;5-D* [19]. Epigenetics plays an important role in the dosage effect of homeologous transcription [7]. Therefore, the contribution of epigenetics to the lower expressions of *TaHKT1;5-B1* and *TaHKT1;5-B2* should be further studied. Moreover, transcription factors, such as *AtABI4* [23] and *OsMYBc* [24], were shown to regulate *HKT* genes in plants, offering more candidate targets for enhancing salinity tolerance. However, an up-stream regulator(s) of wheat *HKT* genes is still unidentified possibly due to the complexity of the hexaploid wheat genome.

3. ROS homeostasis involved in salinity tolerance of a somatic hybrid introgression line

Wild relatives and related species often carry specific traits with potential for improvement of common wheat [25]. For

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