

# Worth its salt: a histone acetyltransferase gene enhances salt tolerance in bread wheat

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Plants are constantly exposed to abiotic stressors such as salinity, drought, floods, and temperature extremes. Investigating mechanisms to alleviate the effects of such stresses, especially on agriculturally important crops, can increase yield and allow crops to thrive in adverse environments. Soil salinity is one of the greatest environmental factors limiting crop production and is a growing threat in the face of global climate change (Shrivastava and Kumar, 2015). Understanding the biological mechanisms underlying salt tolerance can allow for the development of crop scapable of withstanding harsher conditions.

Reactive oxygen species (ROS) are produced in response to environmental stresses including high soil salinity. Recent research suggests that ROS are more than detrimental waste products and that these molecules are key components in signal specificity with highly regulated production and homeostasis. Additionally, the application of exogenous H<sub>2</sub>O<sub>2</sub> at appropriate concentrations can drastically reduce damage caused by salt stress by triggering the necessary pathways in response to high salt conditions (Zhang et al., 2007; Liu et al., 2014; Zhang et al., 2020).

Studies have highlighted a link between polyploidy and increased tolerance to biotic and abiotic stress (Chao et al., 2013; Yang et al., 2014). Common wheat (*Triticum aestivum* L.), an allohexaploid with genome AABBDD, is naturally more salt-tolerant than its tetraploid (*T. turgidum*) and diploid (*Aegilops tauschii*) progenitors (Berkman et al., 2013; Yang et al., 2014). *Triticum aestivum* combines the AB genomes from *T. turgidum* with the D genome from *A. tauschii* (Berkman et al., 2013). In this issue, Zheng et al. (2021) elucidate the molecular basis of higher salt tolerance in hexaploid wheat, reveal the role a master regulator plays through epigenetic modification to mediate salt stress, and show differences in wheat ploidy indicate variation in salt tolerance.

In the study, the authors identified the *T. aestivum* regulator *Histone Acetyltransferase Gene1* (*TaHAG1*) by comparing

the transcriptomes of a synthetic hexaploid wheat and its allotetraploid and diploid parents when subjected to salt stress. In a previous study, they showed that wheat *HAG1* complemented loss-of-function in *Arabidopsis* (*Arabidopsis thaliana*), increasing the plants' tolerance to salt stress, supporting this gene's role in salt stress tolerance, and indicating clear conservation between monocotyledon and eudicotyledon homologs (Zheng et al., 2019). Here, the role of *TaHAG1* in salt stress response was further validated by creating overexpression (*TaHAG1*-OE) and RNAi and CRISPR-mediated knockout lines and exposing them to saline conditions. The authors revealed *TaHAG1* acetylates H3K9 and H3K14 residues and directly targets three NADPH oxidase genes known as *Respiratory burst oxidase homologs* (*Rbohs*). These three target genes were downregulated in *TaHAG1*-RNAi lines and upregulated in *TaHAG1*-OE lines, indicating *TaHAG1* triggers increased H3K9ac and H3K14ac, resulting in transcriptional upregulation. Likewise, the *TaHAG1*-RNAi lines had decreased H<sub>2</sub>O<sub>2</sub> production while *TaHAG1*-OE lines resulted in H<sub>2</sub>O<sub>2</sub> accumulation, likely in response to decreased and increased expression of the three *Rbohs* target genes, respectively, due to their roles in ROS production. While the exact mechanism remains unclear, *TaHAG1* also promoted the activity of the cytosolic enzymatic antioxidants superoxide dismutase, ascorbate peroxidase, and catalase, allowing the plant to achieve ROS homeostasis and tolerance to salt stress. Under salt stress treatment, the hexaploid plant showed physiological and morphological properties more similar to that of the diploid parent than the tetraploid parent. This suggests increased tolerance to salt stress does not linearly increase with ploidy but is rather inherited from the D genome donor.

Improved response of crop plants to abiotic stresses, such as salinity, is of interest to plant scientists; however, modification to candidate genes often results in compromised growth and subsequent yield loss (Wang et al.,

2019). Previous research suggests the high-affinity potassium transporter *TaHKT1;5-D* could contribute to higher salt tolerance in hexaploid wheat (Byrt et al., 2014), but *TaHAG1* did not influence expression of *TaHKT* genes in this study, demonstrating multiple independent pathways involved in salt stress tolerance. Nevertheless, this study highlights a gene that directly contributes to higher salt tolerance in wheat while conferring a yield advantage when exposed to high salt conditions. *TaHAG1* can be targeted for genetic engineering to improve salt tolerance in other crops as well, allowing for the development of crops that are more tolerant of changing climatic environments.

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