

Accepted Manuscript

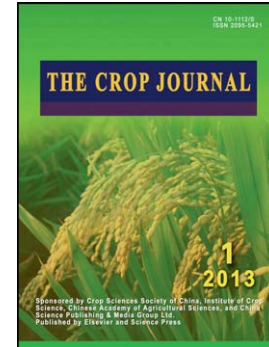
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PII: S2214-5141(17)30096-X
DOI: doi:[10.1016/j.cj.2017.09.005](https://doi.org/10.1016/j.cj.2017.09.005)
Reference: CJ 258

To appear in: *The Crop Journal*

Received date: 29 June 2017
Revised date: 2 September 2017
Accepted date: 10 September 2017



Please cite this article as: Zhongfu Ni, Hongjian Li, Yue Zhao, Huiru Peng, Zhaorong Hu, Mingming Xin, Qixin Sun, Genetic improvement of heat tolerance in wheat: recent progress in understanding the underlying molecular mechanisms, *The Crop Journal* (2017), doi:[10.1016/j.cj.2017.09.005](https://doi.org/10.1016/j.cj.2017.09.005)

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Genetic improvement of heat tolerance in wheat: recent progress in understanding the underlying molecular mechanisms

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Abstract: As a cool season crop, wheat (*Triticum aestivum* L.) has an optimal daytime growing temperature of 15 °C during the reproductive stage. With global climate change, heat stress is becoming an increasingly severe constraint on wheat production. In this review, we summarize recent progress in understanding the molecular mechanisms of heat tolerance in wheat. We firstly describe the impact of heat tolerance on morphology and physiology and its potential effect on agronomic traits. We then review recent discoveries in determining the genetic and molecular factors affecting heat tolerance, including the effects of phytohormone signaling and epigenetic regulation. Finally, we discuss integrative strategies to improve heat tolerance by utilization of existing germplasm including modern cultivars, landraces and related species.

Keywords: Heat stress; Phytohormone signaling; Epigenetic regulation; *Triticum aestivum*

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the world's staple crops, and high and stable yield is the most important target for wheat breeding. As a cool season crop, wheat has as an optimal daytime growing temperature during reproductive development of 15 °C and for every degree Celsius above this optimum a reduction in yield of 3%–4% has been observed [1]. However, the average global temperature is reported to be increasing at a rate of 0.18 °C every decade [2]. Thus, the likely impact of heat stress in wheat has recently attracted increasing attention [3–8]. In this review, we summarize current knowledge about the impact of heat stress on wheat, including the underlying molecular mechanisms and genetic improvement of heat tolerance, especially the results of recent research in China.

2. Heat stress damage to cellular structure and physiology

Heat stress causes damage to cellular structure and affects various metabolic pathways, especially those relating to membrane thermostability, photosynthesis and starch synthesis [9–17]. Denaturation of proteins and increased levels of unsaturated fatty acids caused by heat stress disrupt water, ion, and organic solute movement across membranes, leading to increased cell membrane permeability, and in turn, inhibition of cellular function [11]. High temperature adversely affects photosynthesis in a number of ways [12]. Thylakoid membranes and PS II are considered the most heat-labile cell components [13]. Thylakoid membranes under high temperature show swelling, increased leakiness, physical separation of the chlorophyll light harvesting complex II from the PSII core complex, and disruption of PSII-mediated electron transfer [14]. Thylakoids harbor chlorophyll and damage to thylakoids caused by heat can lead to chlorophyll loss [13, 14]. Starch synthesis is highly sensitive to high

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Received: 2017-06-29; Revised: 2017-09-02; Accepted: 2017-10-09.

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