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Heat stress induced impairment of starch mobilisation regulates pollen viability and grain yield in wheat: Study in Eastern Indo-Gangetic Plains

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ABSTRACT

Delayed sowing of spring wheat due to late harvesting of long duration rice varieties sown in Eastern Indo-Gangetic Plains (EIGP), results in yield loss associated with high temperatures. Present study intended to evaluate the consequences of high temperature on physiology, yield attributes and yield of spring wheat genotypes ($n = 30$) sown in the field for three consecutive winter seasons with different sowing windows; November (timely), December (late) and January (very late). The average temperature during anthesis stage of late (LS) and very late sowing (VLS) conditions were 2.7 °C and 5.2 °C higher than that of the timely sowing (TS) condition, which caused an average yield reduction of 18% under LS and 34% under VLS conditions as compared to the TS condition. Heat stress induced 8.6 days reduction in average grain filling duration under LS and 12.6 days under VLS condition, in turn caused 17 and 39% respective decrease in the test weight. High heritability was observed for tiller no. m^{-2}, spike length, membrane stability index and grain no. $spike^{-1}$ while low heritability for grain yield and thousand grain weight among the genotypes studied. In our study, genotypic variation was obvious in all traits regarding thermal susceptibility. Halna, one of the wheat lines studied, displayed extreme heat tolerance among the considered genotypes with the lowest heat susceptibility index for grain yield ($HSI < 0.5$). NW1012 and Raj4238 presented high yield under TS conditions but could not sustain their ability when exposed to heat stress ($HSI > 1.0$). Furthermore, high temperature driven degradation of chlorophyll probably reduced photosynthetic capacity. Moreover, impaired transport of photosynthate (starch mobilization) from green foliage (source) to anther tissues (sink) leaded to high pollen mortality and thereby decreased grain yield. The results suggested that high temperature caused the significant negative influence on wheat genotypes at anthesis stage establishing a direct association of photosynthesis with starch mobilisation, pollen viability and grain yield. The study also introduced a crop model system for further revelation of the molecular background of thermo-tolerance in plants.

1. Introduction

Gradual increase in intensity of global temperature accompanied by its extended duration is emerging as a potential threat to agricultural productivity and sustainability throughout the world. Intergovernmental panel on climate change (IPCC, 2014) has predicted the constant weather change to increase the frequency of hot days in different parts of the world. The average universal tem-

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Abbreviations: HSI, heat susceptibility index; LS, late sown; MSI, membrane stability index; RWC, relative water content; TS, timely sown; TGW, thousand grain weight; VLS, very late sown.

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perature has beenestimated to be intensifying with a frequency of 0.18 °C every decade (Hansen et al., 2012). Increase in temperature has significant influences on crop productivity and may lead to dramatic yield losses (Dias and Lidon, 2009; Asseng et al., 2015).

Wheat (*Triticum aestivum* L.) is one of the important staple food crop (Dwivedi et al., 2012, 2014). At present, the IGP have been supposed to contribute up to 15% of the universal wheat production (Bita and Gerats, 2013). Wheat is extremely susceptible to high temperature (Dias and Lidon, 2010; Wang et al., 2016). Delayed sowing of wheat exposes its grain filling stage to high temperature (Pandey et al., 2015). Therefore, heat stress imposed to the plants due to delayed sowing is considered as the most significant abiotic stress affecting wheat cultivation in South Asia, predominantly the Eastern Gangetic Plains of India (Joshi et al., 2007a). The optimum temperature required during wheat anthesis and grain filling ranges between 12–22 °C. Exposure to temperature above 30 °C at pre or post anthesis stage reduces the grain filling rate in wheat and thereby decreases grain yield and quality (Stone and Nicolas 1995; Barnabas et al., 2008). Thus, lengthening of the vegetative phase has been found as one of the foremost facts observed in timely sown plants as plants utilise the abundant time for enhancing their height and thus the sugar reservoir (Mondal et al., 2016). Heat stress induced leaf senescence leads to decreased sugar reserve in plants. (Farooq et al., 2011; Tovignan et al., 2016). Genotypic variation for thermal susceptibility has been observed being the reproductive stage the most sensitive. (Joshi et al., 2007b; Dhyani et al., 2013).

Higher ambient temperature affects crops in myriad ways. Elevated temperature leads to a series of physiological and structural modifications in plants (Fahad et al., 2016). Photosynthesis exhibits the maximum sensitivity towards elevated temperature with a significant decrease in the net photosynthetic rate and thereby reducing plant growth (Mathur et al., 2014). Heat stress induced impairment of chlorophyll biosynthesis has been held responsible for reduced accumulation of the chief photosynthetic pigment (Tewari and Tripathy, 1998). High temperature induced inhibition of photosynthesis is often attributed to increased photorespiration rate due to the decreased solubility of O_2 over CO_2 (Long et al., 2004). Declined solubility of gases also upsets the kinetics of the key photosynthetic enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Demirevska-Kepova et al., 2005). Heat stress moreover disturbs activation of rubisco facilitated by rubisco-activase in wheat that in turn decreases photosynthesis (Almeselmani et al., 2012). In wheat, conveyance of assimilate from vegetative tissues to kernel is also affected by high temperature (>30 °C) resulting in poor yield (Plaut et al., 2004). Consequently, accumulation of accessory pigment carotenoid, associated with photo-protective mechanism is also disturbed due to heat stress (Maria de Leonardis et al., 2015). Temperature stress results in decreased stomatal conductance and transpiration rate (Gupta et al., 2015). Temperature requirement of different plants vary for the critical points for plant growth and development. Temperature above 30 °C during floret formation leads to floral abortion in wheat (Wardlaw and Wrigley 1994). Pollen development, viability and fertilization in wheat have been found to be severely impaired by high temperature, which often leads to pseudo seed setting (Young et al., 2004; Kumar et al., 2013). Pollen maturation requires starch as an energy reserve and thus starch accumulated in the stem tissue is exploited as transitory sink during reproductive phase of plants (Zhang et al., 2010). High temperature induced obstacle in starch mobilisation within the anther interrupts pollen development and intensifies pollen mortality (Zhang et al., 2012). Grain yield in crops is critically dependent on successful reproductive development and evaluating pollen viability may be considered as an important criterion in selecting the heat tolerant genotype (Mesihovic et al., 2016).

The present study was commenced to evaluate the impact of high temperature on timely, late and very late sown wheat genotypes. The research included morpho-physiological, anatomical and biochemical characterization and estimation of yield traits of different wheat genotypes for three sequential years with an objective of identifying the thermo-tolerant wheat genotype and establish their thermo-tolerance level.

2. Material and methods

2.1. Weather conditions and experimental layout

The study was executed in winter seasons of 2013–16 at the field of ICAR Research Complex for Eastern Region, Patna, India (25.594°N, 85.1376°E; 53 m above sea level). The region has a humid subtropical climate with a short winter extending from the month of November to March. The meteorological conditions for this site in the course of the study period are presented in Fig. 1A. The soil at the experimental site belongs to the major group of Indo-Gangetic alluvium (sand, silt and clay was 23.4, 39.6 and 37%). Experimental soil was neutral in pH (7.5), electrical conductivity 0.05 (dSm^{-1}), medium in organic carbon (0.6%), low in available nitrogen (213 $kg\,ha^{-1}$), medium in available phosphorus (19 $kg\,ha^{-1}$) and available potassium (416 $kg\,ha^{-1}$). Before the trials, the field was thoroughly labelled with laser labeller and optimum moisture was maintained during the sowing time. Trials were performed in 5.4 m^2 extended plots with 6 rows and 23 cm spacing. Crop management was optimal with fertiliser application, pest control and irrigation to avoid drought condition. Fertiliser was applied in the form of Urea, di-ammonium phosphate (DAP) and murate of potash (MOP) (120N:60P:40 K $kg\,ha^{-1}$). A full dose of phosphorus, potash and 50% nitrogen was applied as basal dose and the remaining 50% nitrogen was applied into equal split doses during the crown root initiation (CRI) and maximum tillering stage.

2.2. Plant materials

An experiment was conducted with 30 wheat genotypes (n = 30) recommended and released for north eastern plains zone (NEPZ) and as suggested by breeder. Wheat genotypes were obtained from Division of Genetics, Indian Agricultural Research Institute, New Delhi. The study was performed during the winter seasons (November to April in India) in EIGP for three consecutive years (2013–2016). Experiments were accomplished in two phases with a first phase of screening and the later phase of elaborate study. Three consecutive experiment seasons comprised of screeningof 30 wheat genotypes based on membrane thermo stability index (MSI), tiller number m^{-2}, spike length, grain number $spike^{-1}$,grain filling duration (GFD), thousand grains weight (TGW) and grain yield (GY). On the basis of first year screening, 6 promising wheat genotypes (DBW14, Halna, HD2733, HD2987, NW1012 and Raj4238) were selected for further detailed characterization on the basis of phenological, anatomical, physiological, biochemical and yield attributes to establish the level of heat stress tolerance among genotypes. Wheat genotypes sown at late-November, mid-December and early-Januarywere considered as timely sown (TS), late sown (LS) and very late sown (VLS) conditions, respectively. The sowing time was optimised in such way that late and very late sown crop face heat stress during reproductive phase. Details of sowing time of 30 genotypes and there phenological stages present in Table 1.

2.3. Sampling time/stage

All the physiological (gas exchange parameters, CTD, RWC), biochemical (chlorophyll and starch content) and anatomical studies