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Review

Field crops and the fear of heat stress—Opportunities, challenges and future directions

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ABSTRACT

Predicted increase in temperature variability can result in short duration of heat stress episodes coinciding with vulnerable reproductive processes leading to significant reduction in floret-fertility in crops. Recent knowledge on alternations in the pollen and stigmatic morphology, pollen biochemical and lipid composition, variable sensitivity of floral reproductive organs and differential temperature thresholds across crops advances the knowledge on heat stress induced reduction in seed-set and harvest index. Rapid increase in night-time temperature, leading to narrowing diurnal temperature amplitude is a major emerging threat to sustain crop productivity. Interestingly, wild wheat (*Aegilops* spp.) with higher heat-tolerance and wild rice (*Oryza officinalis*) escaping damage by completing flowering during early morning hours, are examples of novel opportunities to breed field crops resilient to heat stress. Information on mechanisms leading to heat stress induced sterility is biased towards rice, wheat and sorghum, while the same across other field crops is limited. Hence, increasing research efforts in this direction is critical and timely.

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Contents

1. Introduction

Cereals, millets, oil seeds and other field crops respond differently to short and long duration heat stress exposure during different growth and developmental stages but are most vulnerable during the key reproductive stages i.e., gametogenesis and flowering (Hedhly, 2011; Prasad and Djanaguiraman, 2014; Prasad et al., 2015; Shi et al., 2015; Singh et al., 2015). Under field conditions, these key developmental processes extend over a period ranging between 14 and 21 days depending on crop species. Field crops have different optimum and critical temperature thresholds for achieving reproductive success, beyond which a series of morph-physiological processes determining seed-set are affected leading to significant yield losses. The level of damage caused is based on crop sensitivity, and duration and intensity of heat stress exposure. Continuous efforts in quantifying the impact of heat stress during the sensitive reproductive stage in crops, primarily using controlled environment facilities have identified damaging temperatures lying between 30 and 40 °C (Fig. 1). High day-time temperatures coinciding with reproductive stage can cause significant damage to reproductive processes in cereals (30–38 °C), millets (40 °C), oilseeds (35–36 °C) and pulses (32–40 °C) (Fig. 1). Information on the sensitivity at a finer developmental time scale, accounting for a large proportion of the damage during these vulnerable stages will allow developing precise genetic and molec-

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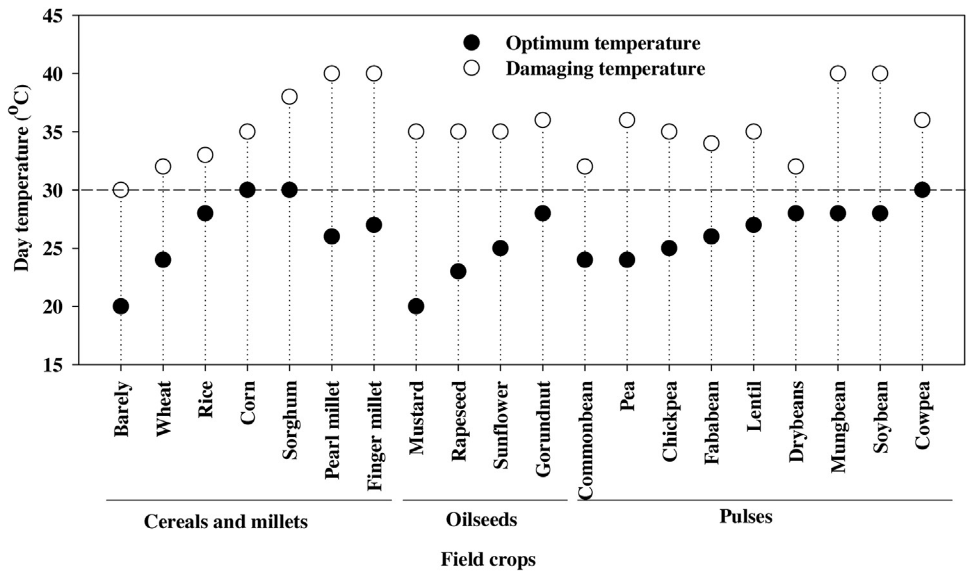

Fig. 1. Day optimum and damaging temperature thresholds at reproductive stage in field crops. Optimum (OT) and damaging temperatures (DT) thresholds for cereals [barely (OT/DT:20°/30 °C, Sakata et al., 2010), wheat (24°/32 °C; Pradhan and Prasad, 2015), rice (30°/35 °C; Satake and Yoshida, 1978), corn (30°/35 °C; Ordóñez et al., 2015), sorghum (30°/38 °C; Nguyen et al., 2013)], millets [pearl millet (26°/40 °C; Gupta et al., 2015), finger millet (27°/40 °C; Opole et al., 2010)], oilseeds [mustard (20°/35 °C; Angadi et al., 2000), rapeseed (23°/35 °C; Young et al., 2004), sunflower (25°/35 °C; Hewezi et al., 2008), groundnut (28°/36 °C; Prasad et al., 2000)] and pulses [common bean (24°/32 °C; Porch and Jahn, 2001), pea (24°/36 °C; Lahlali et al., 2014), chickpea (25°/35 °C; Devasirvatham et al., 2012), fababean (26°/34 °C; Bishop et al., 2016), lentil (27°/35 °C; Singh et al., 2016), drybean (28°/32 °C; Prasad et al., 2002), mungbean (28°/40 °C; Kumari and Varma, 1983), soybean (28°/40 °C; Djanaguiraman et al., 2013) and cowpea (30°/36 °C; Craufurd et al., 1998)], mostly synthesized from controlled environmental studies.

ular interventions to minimize negative impacts of heat stress. The male reproductive organ (anther/pollen or male gametophyte development) have been identified to be the major factor determining seed-set under heat stress, wherein loss of pollen viability and reduced pollen germination percentage on the stigmatic surface leading to sterile flowers has been quantified across crops (Djanaguiraman et al., 2014; González-Schain et al., 2015; Li et al., 2015; Polowick and Sawhney, 1988). Pollen tube growth and development within female tissue, following pollination have documented sensitivity to heat stress in wheat (Saini et al., 1983), cotton (Snider et al., 2009, 2011), chickpea (Kumar et al., 2013), rice (Jagadish et al., 2010) and other crops (Kaushal et al., 2016, references within). However, in majority of the self-pollinated crops, there is limited information on heat stress impact on the female reproductive organs (pistil – stigma, style and ovary), which warrants further detailed investigation. In addition, other mechanistic aspects such as variation in the pollen and stigmatic surface morphology, pollen and anther lipid composition, pollen reactive oxygen species (ROS) production damaging their membrane are either not known or less studied in most field crops.

Season-long high-temperature stress decreases biomass production, seed number, individual seed weight and yield of all grain crops, which is reflected in the harvest index (HI = grain yield/total aboveground biomass). Knowledge on temperature thresholds that can differentiate field crops with higher HI will provide additional options for deploying resilient replacement crops in scenarios faced with heat stress challenges. Another component of the climate change phenomena is the rapid increase in night temperature resulting in narrowing diurnal temperature amplitude. Recent studies indicate significant negative impact of high night temperature on yield and grain quality among field crops (Bahuguna et al., 2016; Garcia et al., 2015, 2016; Lyman et al., 2013; Prasad and Djanguiraman, 2011; Narayanan et al., 2015; Shi et al., 2013; Sunoj et al., 2016; Welch et al., 2010). Warmer nights negatively affect the balance between photosynthesis and night respiration rates, reducing the overall carbohydrate pool and biomass leading to reduced yield and lower HI (Bahuguna et al., 2016; Garcia et al., 2016; Shi et al., 2013).

Breeding efforts focused on increasing yield have gradually minimized or in some cases outbreed the plasticity for stress response, rendering crop production vulnerable to climatic changes. Different mechanisms have been identified to minimize heat stress damage during flowering in rice, including heat escape (early morning flowering; Ishimaru et al., 2010; Julia and Dingkuhn, 2012; Hirabayashi et al., 2014), heat avoidance through transpiration cooling (Julia and Dingkuhn, 2013) and heat tolerance through resilient reproductive processes (Jagadish et al., 2010). Such systematic quantification of mechanisms or traits in other crops is unclear. Additionally, options to sustain genetic gains and simultaneously increase resilience to heat stress is possible through exploring diversity in wild species for heat tolerance (example – wheat; [Pradhan et al., 2012; Pradhan and Prasad, 2015]). Hence, this focused review highlights the progress achieved in quantifying the degree of sensitivity on a developmental time scale during the reproductive phase, comparative assessment of floral organs vulnerability and varying temperature thresholds inducing changes in harvest index (HI) in different crops important for global food security. Opportunities available through exploring wild species and research direction for crop improvement to sustain global food production under future hotter climates are highlighted and discussed.

2. Reproductive stage vulnerability on a developmental time scale

On a broader developmental scale, reproductive stages in field crops are known to be more susceptible to heat stress compared to vegetative stages. However, the finer window of sensitivity during reproductive stages particularly flowering is less known across different crops. Among cereals such as wheat and rice, the duration taken by a spike, head or panicle, respectively to complete flowering is about 5–6 days and across different tillers (in rice) may