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Advanced screening and breeding approaches for heat tolerance in wheat

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Abstract

Food and nutritional security will be decline by consequent changes in climate condition. Global warming is predicted the frequency and severity of heat stress. Global climate change risks are expected that global mean temperature increase at 0.3% per decade. Wheat is very sensitive to heat stress, it is a complex function of heat intensity, duration of exposure, rate of rise in temperature. It is the most widely cultivated cereal crop in the world so play an important role in food security. Wheat have different responses at different developmental stages to heat stress, during vegetative, reproductive and grain filling stage. For instance, inhibit germination, seedling subjected to short term heat stress showed reduction in dry mass, shoot and root length. Physiological responses waters relations, accumulation of compatible osmolytes, heat stress often leads to the generation of reactive oxygen species (ROS). Heat tolerance- ability of some genotypes to better perform than others when their internal temperatures are comparable and in the realm of heat stress. Plants also implement various mechanisms against HS such as ion transport, osmoprotectants, maintenance of membrane stability, scavenging of ROS. Screening methodologies for heat tolerance that are cell membrane thermo-stability test, chlorophyll content, canopy temperature depression (CTD). Breeding strategy for heat tolerance crops, conventional breeding, strategies employing traditional breeding protocols to develop heat tolerant crop. Genetic improvement for heat-stress tolerance, these responses accommodate short-term reaction and tolerance to specific stresses, molecular marker technology and genetic transformation, have resulted in genetic characterization and development of plants. The application of quantitative trait locus (QTL) mapping has contributed to a better understanding of the genetic relationship among tolerances to different stresses. Biotcnological approaches to study and improve plant stress tolerance include MAS and genetic transformation.

Keywords: Global warming, Heat stress, Heat tolerance, Osmoprotectants, Breeding strategy, Quantitative trait locus mapping, MAS, Genetic transformation

Introduction

The major problem of this century is to produce sufficient food to meet the increasing population (10 billion by 2050) despite reductions in quantity and quality of arable land, water availability and increasingly variable weather patterns that are associated with climate change (Mickelbart *et al.* 2015) [34]. FAO estimated that the world requires additional 198 million tones of wheat by 2050 to accomplish the future demands, for which wheat production need to be increased by 77% in the developing countries (Sharma *et al.* 2015) [44]. Wheat is major stable crop about 30% of the world's cereal area to provide food for 36% of the world population (Cossani & Reynolds, 2012) [10]. Wheat is providing around 20% of calories and proteins in human diet. Since 1980s, global wheat productivity is estimated to have been reduced by much as 5% due to heat stress (Lobell *et al.*, 2008) [30]. Such increase of global temperature may have a significant influence on productivity in accordance with the severity of the high temperature, drought, salinity, waterlogging, and mineral toxicity stresses. High temperature-induced heat stress is expressed as the rise in air temperature beyond a threshold level for a period sufficient to cause injury or irreversible damage of crop plants in general (Teixeira *et al.* 2013) [46]. The heat stress situation is aggravated when soil temperature increases as a result of increase in air temperature associated with decline in soil moisture. Thus, heat stress has appeared as a great threaten to successful crop production in the world (Kumar *et al.* 2012; Lobell and Gourdjji 2012; Gourdjji *et al.* 2013) [29, 31, 16].

Global climate change harms are expected to be as high as global mean temperature increase of ≥ 4 °C would posture large prospects to global and regional food security (IPCC. In Field CB *et al.* 2014). Hence, adopting some strategies such as reforestation, water harvesting in field and households, optimal use of CO₂ emitting devices like cement production, burning of fossil fuels like coal, oil and natural gas etc., are essential, but as they are dependent on government policies, it is difficult to achieve them in short term. For long term, the adoption of

extinct native crops and its diversity in individual farm is highly required to meet not only the food and nutritional security but also the feed security for farm livestock (Raju *et al.* 2013)^[39].

Wheat production in India had observed a quantum jump from 6.5 million tones in 1950 to 98.30 million tones in 2017. Yield loss of 33.6% was observed in wheat crop due to high temperature in late sown varieties that indicating a need to development heat tolerant cultivars in wheat for achieve sustainable production (Joshi *et al.* 2007)^[27]. Besides terminal heat, early heat is also posing barrier for sustainable yield. In north-western and central India farmers are shifting to earlier sowing to take advantage of residual moisture. This helps to escape terminal heat stress occurring at the end of march. More efficient screening procedures are key traits in tolerant lines they essential toward breeding for heat tolerance. It evaluated by a variety of viability assays, measurements and testing by different methods (Yadav *et al.* 2011)^[53]. Breeding for heat tolerance include wide variation has been noted in both cultivated and related wild species among different crop plants. The wild relatives may have higher level of tolerance to abiotic stress, but their incorporation into cultivated background needs a perfect prebreeding or backcross program (Mickelbart *et al.* 2015)^[34]. Molecular markers and transgenic approaches have been suggested for heat tolerance in wheat.

Plant responses to heat stress

Morphological symptoms

Temperature plays an important role in all stages of wheat such as seedling emergence, vegetative stage, flowering/reproductive, and grain filling stages. At high temperature have been observed such as scorching of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition and grain filling duration reduced that leads to decreased plant productivity (Hossain *et al.* 2013)^[22].

Anatomical changes

At high temperatures, severe cellular injury and even cell death may occur within minutes, which could be attributed to catastrophic collapse of cellular organization. Direct injuries due to high temperatures include protein denaturation and aggregation, and increased fluidity of membrane lipids. Indirect heat injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation and loss of membrane integrity (Balla *et al.* 2012; Hampton *et al.* 2013)^[4, 19].

Physiological response

Heat stress induce changes in respiration and photosynthesis and thus leads to a shortened life cycle and diminished plant productivity. A major effect of heat stress is the reduction in photosynthesis causes decreased leaf area expansion, premature leaf senescence, they associated reduction in wheat production (Mathur *et al.* 2014)^[32]. In photosynthesizing tissues, photosystem-II is much responsive to heat stress, the sensitivity of photosystem-II where increasing fluidity of thylakoid membrane and transport of electron to heat stress are observed (Prasad *et al.* 2008)^[38].

Molecular response

Wheat crop have many injuries at molecular level, these injuries eventually lead to starvation, inhibition of growth, reduced ion flux, production of toxic compounds and reactive oxygen species (ROS) including singlet oxygen (O₂), superoxide radical (O₂⁻), hydrogen peroxide (H₂O₂) (Marutani

et al. 2012; Suzuki *et al.* 2012)^[33, 45]. Accumulation of ROS in plasma membrane with depolarization of cell membrane, activation of ROS producing enzyme RBOHD and causes cell death (Mittler *et al.* 2011)^[35].

Heat tolerance mechanisms in wheat

Plant can survive in hot and dry conditions by combinations of adaptations including avoidance/escape mechanisms through morphological and tolerance mechanisms (Hasanuzzaman *et al.* 2013)^[21]. Heat avoidance- ability of genotypes to scatter the radiation energy and thereby, to avoid a rise in plant temperature to a stress level. Heat tolerance- ability of some genotypes to better perform than others when their internal temperatures are comparable and in the realm of heat stress. Short-term avoidance or acclimation mechanisms include changing leaf orientation, reflecting solar radiation, transcriptional cooling, leaf shading of tissues that are sensitive to sunburn, modified the membrane lipid composition, and expended rooting (Wahid *et al.* 2007)^[49]. Early maturation is found closely related to minimum yield losses in many crop plants, which is mainly due to escape mechanism (Yadav *et al.* 2007)^[52]. In tolerance, tolerant wheat genotypes are defined by maintenance of photosynthesis, chlorophyll content, and stomatal conductance under heat stress, while the yield of these genotypes is maintained through higher seed set, grain weight, and extended grain filling duration (GFD) even at elevated temperatures (Yang *et al.* 2002)^[55]. HT is closely correlated with increased capacity of scavenging and detoxifying of ROS, the maintenance of high membrane thermostability is related to thermotolerance (Hameed *et al.* 2012)^[18]. Tolerance mechanism constituted of molecular chaperones which devote to cellular homeostasis by protein folding, translocation and degradation. Hsp/chaperone such as sHsp and Hsp70 maintain the non -native protein in a competent state by stabilizing protein conformation and preventing aggregation (Wang *et al.* 2004)^[50].

Screening methodologies for heat tolerance

Screening for heat tolerance in the field is very challenging due to interactions with other environmental factors, but a wide variety of relevant traits are available that allows successful selection in the field conditions (Yadav *et al.* 2011)^[53]. Heat tolerance can be evaluated by a variety of viability assays, measurements, visual assessment, and testing under hotspot locations.

Cell membrane thermo-stability test

Cellular membrane dysfunction due to stress leads to increased permeability and leakage of ions, which can be readily measured by the efflux of electrolytes from affected leaf tissue into an aqueous medium. First developed this method by the C.Y. Sullivan in the late 1960s for determine sorghum and maize heat tolerance. This has been used to study cellular thermostability for heat in wheat (Blum and Ebercon 1981)^[7]. The membrane thermostability (MTS) can be measured by this formula: $MTS = (1 - T1/T2) \times 100$, where $T1$ is conductivity reading after heat treatment and $T2$ is conductivity reading after autoclaving (Ibrahim and Quick 2001)^[24]. This has been tested in wheat and others found effective under field condition and thus can be used for screening large number of genotypes.

Chlorophyll fluorescence measurement

In heat stress conditions, significant correlation was observed between loss of chlorophyll content and damage to thylakoid

membranes. Heat damage in chlorophylls tissue can be measured by chlorophyll fluorescence. Chlorophyll fluorescence has been linked to a thermal kinetic window established by enzymatic assay (Burke JJ 1990)^[8].

Estimation of membrane lipid saturation

A higher contribution of saturated fatty acids in membrane lipids increases the lipid melting temperature and prevents a heat-induced increase in the membrane fluidity. Thus, increasing the saturation level of fatty acids appears to be critical for maintaining the membrane stability and enhancing heat tolerance in crop plants (Zhang *et al.* 2005)^[57].

Selection in hot production environments

Heat stress screening, one criteria for selection of site is high vapour pressure deficit (VPD) area where low yield was found associated with high VPD during all the growing season, high maximum temperature during most of the growing season, and low photothermal quotient corrected by VPD in the critical period of grain set before flowering (Reynolds *et al.* 1997)^[41].

Canopy temperature depression (CTD)

Canopy temperature depression one of the most commonly used indirect techniques for measurements of the surface temperature of the canopy that is related to the amount of transpiration resulting in evaporative cooling (Cossani and Reynolds, 2012)^[10]. CT is correlated with many physiological factors such as stomatal conductance, leaf area index, plant water status, transpiration rate and crop yield. A hand-held infrared thermometer (IRT) used to measuring canopy temperature. In the heat stress conditions, CTD is related to vascular capacity, cooling mechanism, and heat adaptation (Reynolds *et al.* 1994)^[40].

Advanced breeding approaches for heat tolerance

Breeding approaches for heat tolerance in wheat, the first search for tolerant sources should begin among the modern cultivars/advanced breeding lines and landraces of the species. The further search should be shifted to primary and secondary gene pool in sequence. Their efficient utilization of the identified sources, the need to understand the underlying component traits, their inheritance including genes/QTLs and also association among important traits. All this information generated would facilitate targeted breeding for heat tolerance in crops.

Conventional breeding approach

Conventional breeding approach toward development of heat tolerance cultivars are comparatively less effort among different crops. Exploration and utilization of new genetic variation is the preference for genetic improvement of heat tolerance in wheat breeding programs. In a case study of more than 1200 Mexican wheat landraces collected from areas with different thermal regimes, a highly significant correlation between leaf chlorophyll content and 1000 grain weight was observed and a group of superior accessions were identified. Populations of wild species frequently possess high intra-species variation for tolerance traits. Generally, *Triticum dicoccoides* and *T. monococcum* have been reported as better sources of germplasms that can be used to enhance heat tolerance in bread wheat. Further, variability for heat tolerance were observed in *Aegilops speltoides*, *Ae. longissima* and *Ae. Searsii*. Despite, only a small portion of the reported genetic variation in heat tolerance has been

utilized due to limitations of conventional breeding methods. But, the emphasis has been quite recent and some efforts are being made in few important crops such as wheat, rice, maize, tomato and potato etc. In durum wheat, heat escape an alternative mechanism through which plant completes its life cycle before heat stress condition, this property has been utilized in development of early maturing genotypes such as Waha-1, Omrabi-5, and Massara-1 (Al-Karaki 2012)^[1]. A Tausch's goatgrass (*Aegilops tauschii*) was successfully used as a donor for incorporating HT-relevant component traits such as cell membrane stability and chlorophyll retention into cv. PBW550 through backcrossing (Sehgal *et al.* 2011)^[43].

Biotechnological approach for improving heat tolerance

Transgenic and genetic engineering approaches used for alleviate the negative effects of heat stress by improving heat tolerance in wheat. It involves incorporation of desired gene from one species to another to enhance potential of crops (Zheng *et al.* 2012)^[58]. The constitutive expression of EF-Tu in transgenic wheat protected leaf against thermal aggregation, reduced thylakoid membranes disruption, enhanced CO₂ fixation (Fu *et al.* 2012). The development of transgenic for HT, mainly the focus on engineering genes that encode transcription factors (TFs), chaperones, HSPs, organic osmolytes, antioxidants and plant growth regulators (Grover *et al.* 2013)^[17]. Engineering promoters will facilitate gene pyramiding through genetic modification, addressing the issue of tolerance to multiple stresses at different plant growth stages (Datta *et al.* 2002)^[11].

Molecular aspects of heat tolerance

Some physiological and biochemical traits associated with heat tolerance in wheat are quantitative nature, deciphering them into independent through marker-assisted breeding. With respect to tolerance responses of reproductive tissues, approaches to discover the molecular mechanisms conferring heat tolerance during pollen development are valuable a venue help develop heat-tolerant germplasm. Genome-wide strategies are being used to investigate all aspects of pollen development, including responses to temperature stress. Several studies disclosed that some HSFs are analytic for thermotolerance, but some others play a less critical role (HSP101, HSA32, HSFA1, HSFA3), since knock out variants of these proved to have little impact on tolerance to heat. These results also specify that a complex regulatory network delivers a distinctive protection from heat stress. A latest study shows that in the absence of the HSFA1 transcription factor, a minimal yet significant level of obtain thermotolerance can still be achieved in Arabidopsis mutants. Nevertheless, HSPs are of particular importance in thermos tolerance reactions and act as molecular chaperones to prevent denaturation of target proteins as well as facilitating protein refolding. Several studies reveal that HSPs are not the only players involved in response to heat in the reproductive structures, but other components are involved as well, such as hormones and antioxidants.

Molecular genetic markers are an effective tool that is used to analyse plant genomes and how heritable traits associate to their underlying genetic variation. Sequence-based (microarrays) or anonymous molecular marker systems such as, amplified fragment length polymorphism (AFLP) are often employed in applications of modern plant genetic analysis. Moreover, there inducing cost of DNA sequencing and increasing availability of large sequence data sets will allow quarry for large numbers of such markers. Besides, the

markers can be introduced in genetic linkage analyses and trait mapping, association studies and marker-assisted selection. In the major crops, including those that could deliver the largest impact on improvement of yield security under the expected higher global temperatures, resequencing will become the method of choice for identifying markers that co-segregate with temperature tolerance traits. The wealth of marker data generated by WGS, facilitates the implementation of these very higher resolution marker data sets for quantitative trait locus (QTL) mapping and genome-wide association studies (GWAS). Multiple loci for heat tolerance have been identified in wheat. Two microsatellite markers, Xgwm11 and Xgwm293 associated with grain filling duration using single marker analysis (Yang *et al.* 2002) [55]. Since stay-green phenotype has implication on yield potential of wheat, mainly when assimilates are limited under heat stress, QTL associated with the stay-green phenotype and delayed senescence (Vijayalakshmi *et al.* 2010) [48]. In wheat, SNP marker that clearly distinguished heat tolerance and heat-sensitive cultivars was identified (Garg *et al.* 2012) [15]. For grain-filling rate (GFR) that governs grain yield in wheat under HS, 12 closely linked SSR markers were identified (Barakat *et al.* 2012) [5].

Omic approaches in breeding of heat tolerance

The appearance of highly throughput “Omics” approaches has proceeding a successful period of plant molecular techniques for accommodate to changes in the environment. Latest development in ‘omics’ after post genomic era such as next generation sequencing, modelling of different physiological and molecular understanding, genome scale molecular analysis, and correlation of these molecular analysis with physiology of the plant provides an execute move to adaptability and productivity under heat stress. Latest approach of next generation sequencing methods made possible sequencing the plant species completely useful (Weckwerth *et al.* 2011) [51]. In an Allohexaploid bread wheat

($2n=6x=42$, AABBDD genomes) is one of the complex genomes in which homologous chromosomes having similar genes could complicate the recreate process of biological networks. A draft of wheat genome is completed which shows more than 124,000 gene loci which covers all the sub-genomes (A, B, and D) and proves useful in identifying genes which control biological process. Advance utilization of transcriptomics (RNA-seq) and proteomics will help in describe their functions at gene and protein level respectively. In wheat, expressed sequence tag databases showed that homologous genes can be seen expression in one but remain silent in one or both are rest genomes in the analysis of gene expression. In heat stress conditions in variety of plants, microarray is one of the affluent method for the genome wide transcript expression profiling and is extensively used to generate transcriptional profiles.

Transcriptome profiling for heat tolerance

In wheat, expressed sequence tag databases exhibit that homologous genes can reveal expression in one but remain silent in one or both of the endure genomes in the analysis of gene expression. The high-throughput examination of gene expression is being empower by deep genome sequencing technology (RNA-Seq) which confirm to be successful technique to identify definite changes in the genome (Mochida *et al.* 2004) [36]. Next-generation sequencing technology is in the emerging phase in plant studies but it is divine to replace microarray technique due to its precise results. Due to lack of fully sequenced and complex genome (hexaploid) in wheat present many difficulties to “OMICS” studies.

Proteomics for heat tolerance

It is crucial to study proteome alterations at heat stress conditions as proteins play an important role in plant stress response. The antecedent plant response to stress conditions is the cellular processes stress sensing and signaling processes.

A list of wheat proteomic studies focused on response to heat tolerance

| Stress Condition | Cultivar | Organ | Stress induced modulation of metabolic pathways | Differentially expressed | protein classification | Reference |
|------------------|---------------|-----------|---|--|---|------------------------------|
| Heat and Drought | Vinjett | Kernel | 2-DE, MALDI TOF | Carbohydrate (Glycolysis) | CarboMet, STP | Yang <i>et al.</i> (2011) |
| Heat stress | Butte | Endosperm | 2-DE, QSTAR PULSAR TOF | Carbohydrate Metabolism | CarboMet, NitMet, ProtMet, StrRes, STP, SigTran, Tranp, Trans | Hurkman <i>et al.</i> (2009) |
| Drought | Opata, Nesser | Root | iTRAQ | Energy metabolism, Replication, Repair | EnStr, Oxired, Trans | Alvarez <i>et al.</i> (2014) |

Metabolomics advances for heat stress

Metabolites deliver the energy that is essential for metabolism and growth of protoplasm as they are basic elements of different structural and enzymatic molecules. Metabolites not only work for as a link between phenotype and genetic information but also play a role in determining the physiological condition of organism (Bino *et al.* 2004) [6]. The advances in metabolomics, the availability of whole genome sequence, genome-wide genetic variants, and cost-effective genotyping assays has opened exciting doors to blend metabolomics with crop breeding programs. Mass spectrometry (MS) and nuclear magnetic resonance (NMR) spectrometry proved to be successful technologies (Fernie and Schauer 2009) [12].

Phenomics for heat tolerance

Extensive sequence information is being generated through new-generation high-throughput DNA sequencing

technologies. But, accurate and high-throughput phenotyping of the traits on a large scale remains arduous (Cobb *et al.* 2013) [9]. Currently, high-resolution thermal imaging system was used to effectively measure the leaf temperature. The phenotyping platforms established to screen for HT that include “HTpheno” for image analysis and “Rootscope” used to quantify heat-shock responses in plants (Hartmann *et al.* 2011; Kast *et al.* 2013) [20, 28]. The different images of each plant are recorded and then evaluated using advanced image analysis algorithms to predict plant with certain phenotypes (tuberosa *et al.*). In future, the new generation phenomics platforms would allow cost-effective and user-friendly screening for HT in crop plants.

Conclusion

Plants exhibit a variety of responses to heat stress, which are depicted by symptomatic and quantitative changes in growth, morphology, physiology and biochemical levels. Despite

carrying out intensive studies on the deleterious effects of heat stress in wheat, in depth understanding of the mechanism of heat tolerance is vital for developing tolerant cultivar. High temperature affect plant growth at all developmental stages, later phenological stages, particular anthesis and grain filling. Other notable effect of heat stress anatomical changes in tissues and cell organelles, lipid peroxidation via the production of ROS. Tolerance to heat is difficult to assess in the field due to variation in the timing and severity of natural heat event so, cost effective and rapid screening tool should be in place for applied crop breeding. Therefore, plant breeders should get well prepared with understanding mechanisms of heat tolerance in crops and transferring it to plants with the help of physiological, biochemical and molecular tools. Also, while some striking progress has been reported as to the development of heat tolerant cultivar via traditional breeding, molecular markers, biotechnological and phenomics approaches. Since heat tolerance in wheat is complex processes involving network of genes and pathway, powerful tool such as genomics and marker- assisted recurrent selection are required to be implemented.

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