

High Temperature Stress Tolerance in Maize (*Zea mays* L.): Physiological and Molecular Mechanisms

Yogesh Kumar Tiwari^{1,2} and Sushil Kumar Yadav^{1,*}

¹ICAR-Central Research Institute for Dryland Agriculture, Hyderabad, India

²PhD scholar at JNIAS-Jawaharlal Nehru Technological University Hyderabad, Hyderabad, India

Received: September 26, 2018 / Accepted: November 12, 2018

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Abstract Maize, third most important staple cereal crop across the globe, has been threatened with different environmental constraints including heat and water deficit stress. Higher environmental temperatures negatively affect the most at anthesis, silking and grain filling reproductive phenophases. The situation is further complicated by the variable climatic events, resulting in gradual and sometimes sudden increase in environmental temperature followed by irregular rain frequency and intensity, and thus posing a serious threat to global food security. To meet the ever increasing food demand there is an urgent need to develop climate resilient maize varieties and the goal can be achieved by exploiting the pertinent physiological, biochemical and molecular mechanisms. By introducing certain modifications, together these mechanisms can help us to combat the negative impact of high temperature stress. This review encompasses many of such physiological and molecular approaches which may help in mitigating the adverse effects of heat stress on maize yield. Molecular, biochemical and physiological knowledge available in domain that may be employed in breeding approaches to develop heat tolerant maize genotypes, has thoroughly been discussed.

Keywords: Antioxidants, Climate change, Heat stress, Maize, Photosynthesis

Introduction

Diverse environmental challenges pose a serious threat to food production for the burgeoning human population. Development of genotypes with enhanced abiotic stress is

necessary for the rainfed crops since climate of these regions is very fragile, seriously affecting crop production and productivity. With increasing understanding of biochemical pathways and mechanisms that contribute to plant stress response, it has become evident that many of these responses lead to universal protective mechanisms which are activated by salt, drought and temperature and other signaling pathways. Among the various abiotic stresses, drastic temperature fluctuations are very common during plant growth and development. High temperature stress especially during reproductive phenophase is becoming a major area of concern for plant scientists under fast changing climatic scenario, affecting crop production and productivity worldwide. High temperature stress induces cellular changes leading to overproduction of reactive oxygen species (ROS) which damages nucleic acids, proteins and lipids eventually consequential cell death. Anti-oxidative stress metabolism in plants comprising of enzymatic and non-enzymatic antioxidants imparts stress tolerance by scavenging or detoxification of excess ROS. Better understanding of all the intricacies of anti-oxidative stress metabolism will help in designing appropriate strategies to develop crop plants with enhanced high temperature stress tolerance.

New approaches are being developed to manipulate expression of functionally related classes of genes by maneuvering signaling pathways of abiotic stress and characterization and cloning of transcription factors that regulate the expression of many genes that could contribute to stress tolerance (Ma et al. 2016).

Maize (*Zea mays* L.) is one of the most versatile emerging C₄ crop having wider adaptability under varied agro-climatic conditions across the globe. Globally, maize is known as queen of cereals because it has the highest genetic yield potential among the cereals. It is cultivated on around 177 million hectares worldwide (FICCI 2014) and production during 2016-17 was 1067.21 million tonnes. Despite of its

*Corresponding author; Sushil Kumar Yadav
Tel : +91-9492042651; 91-40-24530161
E-mail : sk.yadav2@icar.gov.in

global reach United States is the highest maize producing region (377.5 million tonnes). As per the 2014 FAOSTAT data, India with 42.3 million tonnes is the fourth largest maize producing country. It is the third most important food crops after rice and wheat in India and one of the fastest growing crop commodity. It can be consumed in a variety of ways by both human and animals. Maize can be used for the production of ethanol, animal feed, cooking oil, syrups, starch and many other useful products. Nutritionally maize contains around 24% carbohydrates, 18% protein and 7% fat. It is also a good source of phosphorus, magnesium, manganese, zinc, copper, iron, Vitamin A, B1, B2, B6, C, E, Niacin, Folate and Pantothenic Acid. In addition to its nutritional, industrial and agronomic importance maize is an attractive model plant species. In comparison to other cereal model plants, maize model has been studied most thoroughly and been a model plant for genetic studies over the past one century. A vast range of maize characteristics, a huge collection of mutant stocks, large heterochromatic chromosomes, extensive nucleotide diversity, and genic co-linearity within related species, have made it a keystone species for genetic, cytogenetic, and genomic studies (Strable and Scanlon 2009). All these attributes made maize to be the prime choice for identifying its potential to the variable climatic variables.

Climate Variability

Sudden changes in environmental conditions adversely impact the agriculture productivity. Prominent among these environmental factors include rainfall and water, light, temperature, relative humidity, air and wind. Other abiotic components, including topography and soil also influence plant growth and development. High temperature influences all plant growth processes such as photosynthesis, respiration, transpiration, breaking of seed dormancy, seed germination, protein synthesis, and translocation. At high temperatures the translocation of photosynthate is faster so that plants tend to mature faster. Climatic variability leads to abrupt changes rise in temperature (predicted rate expected is 0.2-0.4°C per decade) and is likely to add 1.8 to 4°C in present day temperature by the turn of this century. Significant coherent increasing trends in mean temperature were observed in Southern states of India (Rathore et al. 2013). The major threat of variable climate is to developing countries due to scarcity of resources (Noor 2017) and unavailability of real time weather information to the poor farming communities (Ahmad et al. 2016; Brown et al. 2018). Variable climate would be more disastrous for marginal and lower income farmers as compared to progressive and rich farmers.

Greenhouse gases are the main and major culprit of changing the climate, especially for the increase in atmospheric

temperatures. World has witnessed excessive heat events previously and there are predictions of their recurrence more frequently in coming decades (Semenov and Halford 2009). As per model studies it is estimated that sudden extreme environmental events will suppress agricultural yields. On an average escalation of 3-4°C in environmental temperature, there will be a reduction of 25-35% in crop yield in Middle East (Ortiz et al. 2008) and 15-35% in Africa and Asia (Ortiz et al. 2008). Currently, maize is mostly grown in regions with prevailing 18-27°C optimum temperatures. However, it can also be grown at 33-38°C with optimum yield. Temperatures beyond 38°C will drastically impact the economic yield of maize (Koirala et al. 2017).

Heat Stress

Heat stress (enough high temperature for a certain period) can induce irreversible damage to crop plants growth and economic yield (Wahid et al. 2007; Fahad et al. 2017). High temperature can alter metabolic events at cellular level and pollen dehiscence, pollen fertility, silk emergence and stigma receptivity, seed setting and grain filling (Xiao et al. 2011), ultimately reducing the grain yield. Excessive heat also causes the reduction in net photosynthesis, leaf area, reduced biomass accumulation and 1000 seed weight (Shah and Paulsen 2003; Cheikh and Jones 2006). Environmental temperatures higher than optimal may impede both vegetative as well as reproductive growth. However, reproductive stage (anthesis, silking, grain filling and seed set) is the most sensitive stage which eventually lead to complete sterility and kernel abortion in maize (Shah et al. 2011).

Mechanisms of Heat Tolerance

Stress/heat tolerance is the ability of plants which can evade the negative impacts of high temperature and produce the economic yields at par or near to that of normal conditions (Wahid et al. 2007). Tolerance may vary from species to species and even genotype to genotype within the species. In cereal crops including maize substantial genetic variations exists which can sustain and produce during unfavorable environmental temperature events (Shah et al. 2011; Jat et al. 2016). Unlike motile organisms, plant tolerance is achieved by a number of morpho-physiological, biochemical and molecular adjustments. At cellular level high temperatures trigger the expression of certain genes and increase the accumulation of certain metabolites which may enhance the heat enduring ability of plants and thus heat tolerance (Hasanuzzaman et al. 2013). Being sessile in nature plants have evolved several mechanisms ranging from escape to

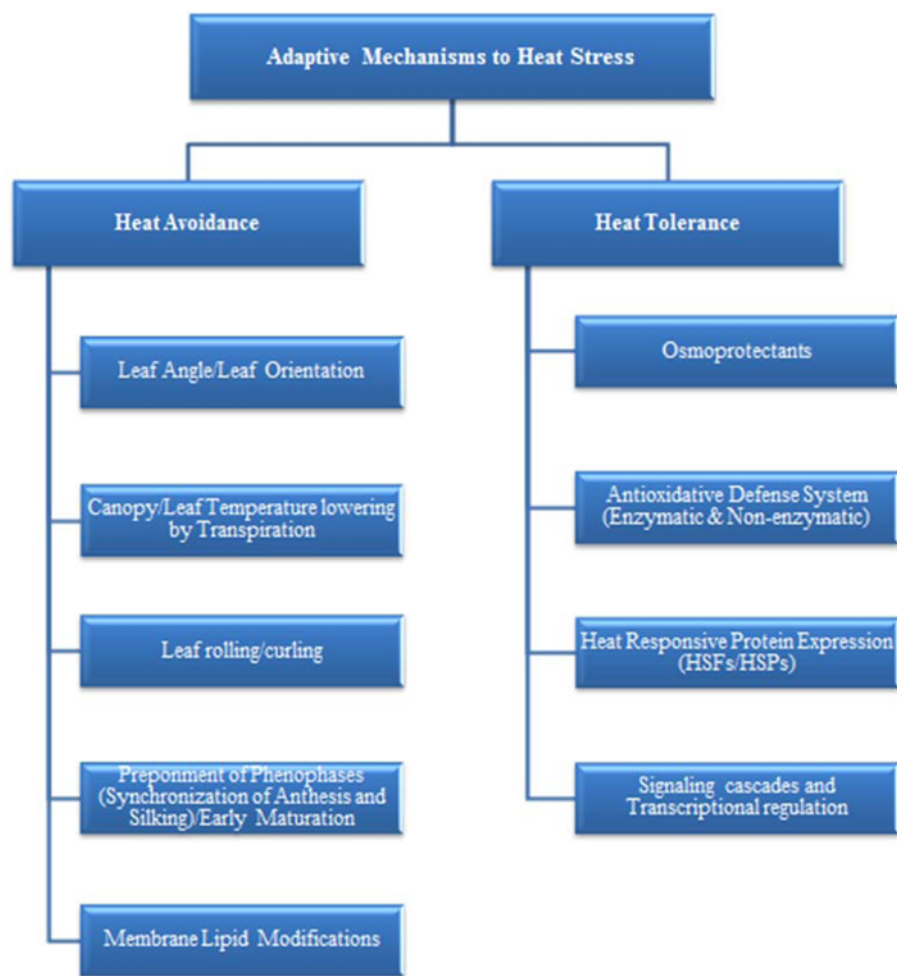


Fig. 1. Mechanisms of Heat Tolerance in Maize plants

avoidance for survival under unfavorable environmental conditions and so for heat stress (Fig. 1). These mechanisms operate both at whole plant level and cellular level. At whole plant level, early maturation, changing leaf angle, leaf thickness, leaf wilting and the like are the stress avoiding strategies. While at cellular level, adjustment processes include ion transporters, LEA proteins, factors participating in signaling cascades, osmolytes, antioxidant defense and transcriptional control (Rodríguez et al. 2005).

Morpho-physiological Adaptations

Stress avoidance primarily achieved by inducing certain changes in plant architecture. For instance, the maize genotypes with high leaf wax, lower leaf angle, compact tassel and lower cob angle are better suited for high temperature stress conditions because of their ability to reduce direct sunlight exposure and the evaporation rate. Reduced evaporation rate in anthers may result in bulging of pollens, a very crucial phenomenon for anther dehiscence (Shah et al. 2011). Pollen

dehiscence at early morning confers heat tolerance by avoidance mechanism in rice (Ishimaru et al. 2015; Bheemanahalli et al. 2017). Therefore, morphological variabilities available in maize germplasm can be used as screening indices.

Heat stress may alter several physiological processes viz. membrane fluidity, net photosynthesis, respiration rate, osmolytes accumulation, hormone levels and so on (Wahid et al. 2007; Waqas et al. 2017). Plants have different strategies to cope with sudden and acquired heat stress. For sudden temperature shoot up; leaf angle, leaf cooling by transpiration and adjustments in membrane lipid composition and distribution are more vital for plant survival (Rodríguez et al. 2005). Apart from this, a number of ionic and osmotic adjustments, induced stress related signals may trigger damage control processes (Vinocur and Altman 2005). Heat tolerance in total is a very complex phenomenon which involves several individual events as well as events in conjugation. Among the physiological adaptations, maintaining photosynthetic rate at optimum even under high temperature stress is the key physiological process that contributes to heat tolerance. Higher rate of

photosynthesis is directly correlated with economic yield and hence enhanced heat tolerance. A report by Yadav and coworkers (2015) suggested that high photosynthetic rate, maintenance of maximum quantum yield PSII photochemistry (Fv/Fm), cell membrane stability and lowering the leaf temperature collectively contribute to heat tolerance in maize.

Biochemical and Molecular Adaptations

High temperatures induce several metabolic events at cellular and sub-cellular level. These events may involve production of ROS and oxidative stress. Oxidative stress is the metabolic stage when production of ROS become more than their neutralization. ROS production occurs at several sub-cellular sites including chloroplasts, mitochondria, peroxisomes, cellular and sub-cellular membranes. ROS are highly reactive in nature and cause damage to membranes, proteins, nucleic acids. Membrane lipid peroxidation is the most destructive and damaging effect of ROS reaction. Peroxidation of membrane lipids increases membrane fluidity and leakage of cellular fluid. This disrupts the cellular homeostasis and eventually cell death. Plants have developed an excellent mechanism widely known as anti-oxidative defense system to protect them from ROS damage. Anti-oxidative defense system includes both enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants include SOD, POD (APx/GPx), CAT, GR and non-enzymatic antioxidants are comprised mainly of tocopherols, β -carotene, ascorbic acid, glutathione and polyphenols.

Stress tolerance is an inclusive and complex mechanism, regulated by several genes at multiples stages during the plant growth (Maestri et al. 2002). Like other cereals, in maize also heat tolerance seems to be regulated by a polygenic system, therefore difficult to exploit its genetics for developing heat tolerant genotypes. Thirunavukkarasu et al. (2017) has reported total number of 174 drought-responsive genes in maize when exposed to moisture stress and their co-expression studies revealed a very vital correlation between several adaptive events, each one representing a specific biological function.

Strategies for Improving Heat Tolerance

It is evident from the literature that substantial progress has been made in individual disciplines like, plant physiology, molecular biology, metabolomics and genomics. By integrating knowledge from these individual domains, strategies can be designed to improve heat tolerance in the already existing genotypes and introduce it in the sensitive ones.

Transcription factors that regulate functionally related genes could be attractive targets for such investigations, since they may also function in regulating quantitative traits. Transgenic manipulation of such transcription factors should help us understand more about multigene regulation and its relationship to tolerance.

Several morphological, physiological, biochemical and molecular markers known to be associated with high temperature tolerance in maize which can further be used for

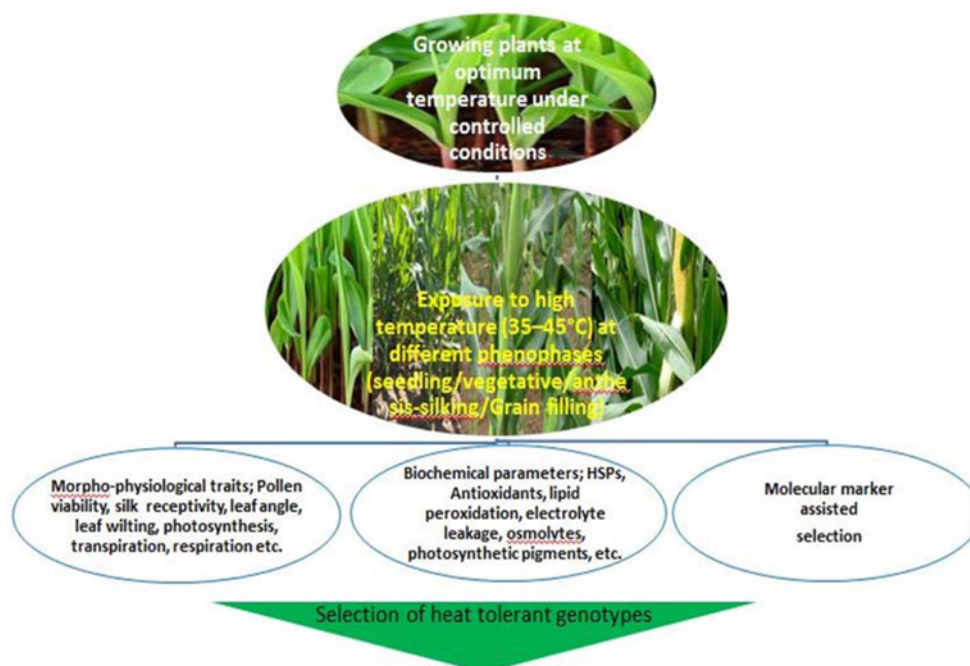


Fig. 2. A schematic representation of steps involved in screening heat tolerant genotypes

developing genotypes with advanced capabilities to thrive and yield better under higher environmental temperatures (Fig. 2).

Morphological Indices

Maize morphological markers for high temperature stress tolerance include pollen fertility, silk receptivity, compact tassel, lesser gap between anthesis and silking (ASI) (Yadav et al. 2012). These parameters along with other physiological markers can be used for the screening of maize germplasm under high temperature stress conditions. Similarly, leaf number per plant, number of cobs per plant, number of rows of seeds per cob, number of seeds per cob, percent kernel abortion, grain yield and 1000-seed weight studied for screening of maize genotypes against heat stress. In previous studies all these characters found to be reduced significantly under high temperature stress (Cairns et al. 2013). Thus, these characters can be considered while screening maize genotypes for heat tolerance in conventional breeding. Anthesis Silking Interval (ASI) is a very useful criterion for enhancing drought tolerance in maize.

Physiological Indices

Net photosynthetic rate, transpiration, stomatal conductivity, leaf surface temperature, canopy temperature depression, maximum quantum yield PSII photochemistry (Fv/Fm) and SPAD are major physiological markers which can be used in screening maize germplasm against high temperature stress. Maize genotypes exhibiting higher net photosynthetic rate, transpiration and stomatal conductance, Fv/Fm and SPAD value with lower leaf surface temperature and cell membrane injury were found to be heat tolerant (Lipiec et al. 2013; Yadav et al. 2016). The high photosynthetic rate coupled with increased Fv/Fm may accumulate more photosynthate leading to improved plant growth. High chlorophyll content in leaves with lower MDA content and electrolyte leakage was observed in maize seedlings possessing higher tolerance to heat stress (Kumar et al. 2012). Similar to electrolyte leakage, leakiness of thylakoid membrane is also increased under moderate heat stress, and this can also be used as screening tool for heat tolerance (Schrader et al. 2004; Sharkey 2005). Also, accumulation of osmolytes like, proline, soluble sugars, phenols, glycine betaine, level of various hormones and water relations have been considered as key physiological parameters for screening against heat tolerance (Wahid et al. 2007). Along with these attributes leaf angle and leaf position, canopy temperature depression through transpiration, membrane lipid distribution and composition and membrane fluidity are some additional parameters which need to be studied for screening of maize against heat stress tolerance.

Biochemical Indices for Heat Tolerance

Antioxidants

At cellular level higher environmental temperatures induce production of highly reactive and toxic oxygen molecules (Apel and Hirt 2004). These active oxygen molecules damage different cellular and sub-cellular membranes; macromolecules and thus disturb the cellular homeostasis (Noctor and Foyor, 1998). However, plants have developed a defense system against the oxidative stress comprising several proteins, enzymes, vitamins; secondary metabolites which are collectively called as antioxidants (Apel and Hirt 2004). Several studies reported that increased antioxidants level promote high temperature tolerance in plants. Plants may mitigate negative effects of heat stress by modulating activity of different anti-oxidative enzymes or by increasing the production of non-enzymatic antioxidants (Almeselmani et al. 2006; Zandalinas et al. 2017). Anti-oxidative enzymes protect plants from oxidative stress by neutralizing the toxic oxygen species. Non-enzymatic antioxidants either act as signaling molecules, enzyme cofactors or directly participate in redox reactions. Ascorbate being a cofactor for various enzymes regulates several physiological and signaling events (Smirnoff and Wheeler 2000; Barth et al. 2006). Ascorbate also regulates the biosynthesis of secondary metabolites like tocopherols (Gallie 2013). Despite of having negative impact on plant growth and development H₂O₂ acts as signaling molecule and triggers several stress responsive events in plants (Hossain et al. 2015). Exogenous application of H₂O₂ was observed to ameliorate negative impact of heat stress in maize plants (Gong et al. 2001; Yadav et al. 2017).

Heat Shock Proteins

Besides several metabolic responses, heat stress results in the increased synthesis of a special set of proteins. These special set of proteins are Heat Shock Proteins (Schulze et al. 2005). Under high temperature, synthesis of normal proteins gets decreased. Heat Shock Proteins are classified into five conserved classes on the basis of their molecular weight viz., Small Heat Shock Proteins (sHSPs, with a molecular mass of 15 to 42 kDa), HSP60, HSP70, HSP90 and HSP100 (Bharti and Nover 2002; Schulze et al. 2005). HSPs major role is maintenance and are also involved in keeping native conformation of other proteins. In this way HSPs improve protein stability under stressed environments (Wahid et al. 2007). HSPs encountering heat tolerance role in plants was first assumed by Vierling in 1991. HSPs role in providing high temperature tolerance is well established fact and is supported by several studies across various living organisms. Major HSPs reported in maize are HSP101 (Nieto-Sotelo et

al. 2000) and sHSPs (Heckathorn et al. 1998).

Osmolytes

In response to unfavorable environmental events, plants activate some adaptive mechanisms and the increased production of osmolytes is most important and one of the well-studied mechanism. These osmolytes may include sugar molecules, proline, glycine betaine and trehalose under heat as well as other abiotic stresses. Several studies showed that the plants having less ability to accumulate these molecules were found to be sensitive to high temperature stress (Rasheed et al. 2011; Yadav et al. 2016). These results were further supported by the studies where exogenous application of osmolytes like proline and glycine betaine reduced the level of oxidative stress and improved the accumulation of soluble sugars thus protected the plants from deleterious effects of heat stress.

Molecular Markers for High Temperature Tolerance

Conventional breeding has made substantial progress in developing heat tolerant crop varieties. However, the genetics of heat tolerance in cereal plants is poorly understood. Several studies focusing on the effect of heat stress on reproductive characters like, pollen viability, silk receptivity, pollen germination, pollen tube growth, grain weight, grain filling and post-anthesis leaf senescence, seed set and quality traits such as dent-flint kernels in maize. In maize, five and six QTLs those regulate pollen heat tolerance (quality and pollen tube growth) have been identified with a high heritability. However, the pollen tests were performed *in vitro* and might not be representative of the situation *in vivo* (Frova and Sari-Gorla 1994). In a study on adult maize under heat stress Frey et al. (2016). identified 11 QTL including 2 loci for heat tolerance with respect to grain yield. Furthermore, they have identified six heat-tolerant and 112 heat-responsive candidate genes co-locating with the previously mentioned QTL. Similarly, maize varieties tolerant to drought and salinity (Ribaut and Ragot 2006; Luo et al. 2017), insect (Samayoa et al. 2015) and diseases (Willcox et al. 2002; Wisser et al. 2011; Humi et al. 2015; Maschietto et al. 2017) were developed by using marker assisted selection (MAS) in breeding. More detailed information for maize QTLs can be explored at <http://www.maizegdb.org> and <http://www.plantstress.com>. However, reports for improving tolerance to heat stress in maize are not very common.

Simple sequence repeats (SSR) and single nucleotide polymorphisms (SNPs) both are widely used in MAS. SNPs are more commonly used markers because of their abundance in genome. Many SNPs associated with heat tolerance in maize have been identified. Each one contributing small-

small towards the variance because of the trait complexity. Therefore it is important to introgress several markers associated with several QTLs into a cultivar to improve its tolerance against heat stress (Messmer et al. 2011; Rodríguez et al. 2013; Frey et al. 2015). Multiple QTLs conferring heat tolerance especially at reproductive stage in maize have been mapped along with their associated markers (Frey et al. 2016). These markers can be deployed in initiating MAS for pyramiding genes to breed for heat tolerance.

Approaches for Evaluating Heat Tolerance

Physiological and Biochemical Approaches

Genotypic evaluation for heat stress under field conditions has always been challenging task because heat is often accompanied with moisture stress conditions. For better understanding of heat tolerance in maize, the evaluation studies should be performed at different growth stages under controlled conditions so that the associated factors may not influence the findings. It is evident that each developmental stage in plants life cycle shows differential sensitivity to heat stress. As compared to reproductive stage, vegetative stage in maize life cycle is less sensitive to high temperature. In a study under field conditions Yadav and coworkers (2015) reported that high temperature during vegetative stage promoted the growth of vegetative plant parts but affected yield-related parameters. Higher temperatures during vegetative growth improved net photosynthetic rate resulting in higher total stover yield at maturity. This yield reduction could be because of reduced pollen viability and source to sink supply of photosynthates. Another study by Yadav and coworkers 2016 on maize seedlings reported a significant decrease in membrane stability, chlorophyll fluorescence and chlorophyll concentration under extended heat stress and sudden heat shock. In another study by Tiwari and Yadav (2016), differential response of antioxidative enzymes under heat stress in maize during reproductive stage was reported. Different antioxidant enzymes; SOD, CAT, APX and POD were found to be associated with heat tolerance in maize. Tiwari and Yadav (2017) reported the role of ascorbate-glutathione cycle in providing tolerance to maize against heat stress at reproductive stage.

Genetic and Molecular Approaches

Several heat responsive genes and proteins have been reported in maize. A number of gene expression studies can be undertaken to confirm role of heat responsive genes. Transcriptomic and proteomic profiles of the heat stressed maize at multiple growth stages can be studied to observe

differential response of genes. Thus the genotypes expressing the genes conferring tolerance to high temperature can be selected for future gene cloning or breeding purposes (Jagadish et al. 2010; Mangrauthia et al. 2016). Constitutive expression of the *Nicotiana* PK1 gene enhanced moisture stress tolerance in maize (Shou et al. 2004). In another transgenic approach, bacterial RNA chaperones conferred moisture stress tolerance in maize plants (Castiglioni et al. 2008). Transgenic maize with enhanced ZmVPP1 expression exhibits improved drought tolerance (Wang et al. 2016). Transgenic maize over-expressing OsMYB55 led to activation of stress-responsive genes and enhanced heat and drought tolerance (Casaretto et al. 2016). Several attempts were made to develop heat-tolerant transgenic maize by manipulating (over-expression/down-regulation) genes of recognized relevance isolated from different crop species including maize.

The already screened germplasm can be explored for studying the molecular mechanisms and used for identifying genetic markers which further can be used in marker assisted breeding. The use of genetic markers as diagnostic tools accelerates the breeding process. Thus the integration of modern genetic engineering practices in traditional plant breeding would lead to develop maize varieties suitable for future growing environments to meet the increasing global food requirements. Rapid progress in next generation sequencing approaches has made the whole process more easy and cost effective. During the regulation of heat stress response in plants, heat shock transcription factors (HSFs) play a very vital role. HSFs control the expression of HSP genes (Chen et al. 2006; Zafar et al. 2016). 25 HSF genes in rice were identified which were observed to regulate the expression of HSPs (Guo et al. 2008). The identification and characterization of HSFs has opened up new avenues for conducting future functional genomic studies. Recently, genome wide association studies (GWAS) has helped in the identification of new QTLs controlling important traits including heat tolerance in crop plants with high accuracy for improved breeding value (Ma et al. 2016; Lafarge et al. 2017). Several genes conferring tolerance to heat and other abiotic stresses at flowering stage have been identified in maize using GWAS which provides a strong basis to breed heat tolerant maize genotypes (Lafarge et al. 2017).

Future Perspectives

Prominent environmental factors which affect crop growth and development include rainfall and water, light, temperature, relative humidity, air and wind. Amongst these drought and high temperature pose a serious threat to sustainable crop production. The negative impacts of climate change can be

minimized by developing heat tolerant crop cultivars possessing multiple abiotic stress tolerance. It needs concerted efforts to develop new crop varieties possess tolerance to major abiotic components via breeding or genetic modification.

Earlier, substantial efforts were made to develop heat tolerant maize by incorporating genes from other conventional genetic resources using traditional methods but the progress has been relatively slow. In the age of modern genetics, it is possible to tap all the available phenotypic diversity contributing towards heat tolerance into the cultivated material through using high throughput phenotyping and genotyping techniques such as GWAS (Ma et al. 2016; Lafarge et al. 2017) and genotyping by sequencing (GBS) (Spindel et al. 2013). The recent emergence of genome editing techniques like CRISPR-Cas9 and TILLING would further accelerate the rate of crop improvement for specific traits like heat tolerance. All these efforts would pave the way for initiating genomics assisted breeding to have genotypes with desired characteristics. However, an integrated approach using multiple techniques for improving complex traits like heat tolerance would be a more appropriate route towards a swift success.

Conclusion

Escalating global environmental temperature due to changing climate would adversely affect the agriculture production across the globe. Plants have evolved several adaptive mechanisms to cope with such environmental stresses. These strategies may involve several metabolic adjustments, gene expression and morpho-physiological alterations. There is a need to explore and characterize genes which are involved in conferring enhanced heat/multiple abiotic stress tolerance. Genes and transcription factors from other plant species, identified for enhancing multiple abiotic stress tolerance can be employed for improving its intrinsic tolerance in maize which is a vital cereal crop grown under very fragile environments. Similarly, the available genotypic variability in maize (re-sequencing the available genetic resources) can be exploited for breeding purpose by means of MAS or by MAS backcross. Other approaches like use of mutagens (chemicals) for altering the gene function can also be given a try for improving tolerance. Possibility of use of advanced genomic assay CRISPR-Cas9 should also be explored in maize for understanding the function of various genes conferring multiple abiotic stress tolerance and high temperature stress in particular. Interface of conventional and modern genomic approaches for mitigating environmental stresses would be the most credible approach for enhancing the high temperature stress tolerance in crop plants including maize.

Acknowledgements

YKT is grateful to Indian Council of Agricultural Research-Central Research Institute for Dryland Agriculture, Hyderabad for providing financial assistance in form of Senior Research Fellowship under National Innovations in Climate Resilient Agriculture project.

Author's Contributions

YKT contributed to the acquisition of information and preparation and revision of manuscript. SKY conceived the idea and made valuable suggestions in preparation and editing the manuscript.

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