



## Mechanisms of heat stress tolerance in maize

Manoj Kandel<sup>1\*</sup>, Surya Kant Ghimire<sup>1</sup>, Jiban Shrestha<sup>2</sup>

### Article Info

Accepted:  
25 Feb. 2018

### Keywords:

Gene action, heat stresses, maize (*Zea mays L.*), tolerance mechanisms

### ABSTRACT

High temperature has become a global concern because it severely affects the growth and production of crops. It causes an array of morpho-anatomical, physiological and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield. Plant growth and development involve numerous biochemical reactions that are sensitive to temperature. Heat stress causes an abrupt increase in the expression of stress-associated proteins which provide tolerance by stimulating the defense response in plants. Plants possess a number of mechanisms to cope with high temperature situations. The adverse effects of heat stress can be mitigated by developing crop plants with improved thermotolerance using various genetic approaches. This article reviews the recent information on responses and tolerance to high temperature stress in maize.

## INTRODUCTION

Plant ability to grow and produces economic yield under heat stress condition is known as plant heat tolerance. Plant has different mechanisms to cope for heat stress condition. They have to show short term and long term evolutionary mechanism for adaptations of heat stress condition. The two mechanism avoidance and acclimation are were not good for long term for adaption to heat stress condition. Ion transporters, late embryogenesis abundant proteins (LEA), osmo-protectants, antioxidant defense are major mechanisms as well as factors responsible for signaling cascades and transcriptional control are important for control and balance the heat stress condition in crop (Rodríguez et al. 2005; Wang et al. 2009). Orientation of leaf, transpiration cooling and lipid composition changes in cell membrane were important for survival under the sudden short term heat stress condition (Rodríguez et al. 2005). Plant different growth stages and their tissue response differently in normal and heat stress condition (Queitsch et al. 2000). Expression of signal in the form of ionic and osmotic effect at initial stage of heat stress responsive mechanisms leads to changes membrane fluidity in order to

survival under heat stress condition. Heat stress tolerant crop reestablishes homeostasis and protein protect and damaged system to cope with the heat stress condition for survival and growth and development.

### Genetics of heat tolerance

In plant breeding prospective heat stress tolerance is a complex quantitative traits and mode of inheritance of traits associated with heat stress prime importance for successful breeding strategies. Heat tolerance also in maize inherited quantitatively, and effective selection for heat tolerance requires evaluating genotypes in replicated trials in multiple environments (Bai 2003). Dominance gene action has been found to be predominant for vigor of seed, germination percentage, growth rate of plant, relative water content, rolling of leaf, anthesis silking duration, pollen size and viability, silk receptivity, shelling percentage, ear number per plant, leaf senescence, plant maturity days and economic yield (Tassawar et al. 2012). Akbar et al. (2008) also reported non-additive gene action for yield and yield contributing characters under high temperature stress in maize. Cell membrane thermo stability percentage, stomata conductance, transpiration rate, turgor potential, growing degree days (GDDs) to 50% tasseling and grain yield per plant are governed by the non-additive genes effect and for growing degree-days to 50% maturity governed by additive genes effect at high and normal temperature condition (Akbar et al. 2009). Traits

<sup>1</sup>Department of Genetics and Plant breeding, Agriculture and Forestry University (AFU), Rampur, Chitwan, Nepal

<sup>2</sup>Nepal Agricultural Research Council, National Maize Research Program (NMRP), Rampur, Chitwan, Nepal

\* E-mail: [manojkandel24@gmail.com](mailto:manojkandel24@gmail.com)

had non-additive or dominant gene action in heat stress condition which could be improved by hybrid breeding strategy to improve heat stress tolerance in maize. Population improvement programs can also increase the frequency of favorable heat tolerant genes in maize populations. Increase composition of sucrose and a large oligosaccharide, raffinose and fatty acid from linoleic acids to oleic acid (18:1) i.e. to a more saturated fatty acids and ultimately leading to improved membrane stability under heat stress condition (Chen and Burris 1990). Application of  $\text{CaCl}_2$  on maize seeding enhance the ABA-induced thermos tolerance by increasing antioxidant enzymes and lowering level of lipid peroxidation. A maize seed pretreatment with  $\text{CaCl}_2$  solution increase of antioxidant system activity and benzyl adenine reduces kernel abortion at tip and middle portion on the ear. Acetyl esterase as positive regulator as well as enhance heat tolerance ability of maize for heat tolerance (Yamamoto et al. 2011).

### Gene expression

In stress tolerance strategy when plant exposure to heat stress condition in molecular level perception of signals changes occur that responsible for expression of gene and formation of transcripts that responsible for formation of stress-related proteins (Iba 2002). In this regard, heat shock proteins (HSPs) expression is one of the most important strategies (Feder and Hoffman 1999). Heat shock proteins behaves as chaperone and function like signal transduction during high temperature condition and its molecular size is in range about 10 to 200 kDa. Plant have different physiological mechanism for survival and growth and development such as photosynthesis; assimilate partitioning, water use efficiency, nutrient use efficiency and membrane stability and these phenomena were control and improved by heat shock protein under heat stress condition for development of thermo tolerance plant (Camejo et al. 2005; Ahn and Zimmerman 2006; Momcilovic and Ristic 2007). Now, molecular breeding as well as genetic engineering as a additional tools for stress tolerance breeding to improved crops yield under heat stress condition.

### Plant morphology and physiology under heat stress

High temperature stress causes adverse effect on plant development, physiological process and grain yield. Heat stress as one of major consequences leads to oxidative stress due to production of excess reactive oxygen species (ROS). High temperature hinder plant growth and development so plant need to continuously struggle for survival (Hasanuzzaman et al. 2013). Under heat stress condition plants changes physical changes and creating signals for alter the different

metabolism to cope high temperature. Crop alter their metabolism through giving compatible solute that responsible to organize protein, cellular structure, keep and maintain cell turgor, changes the antioxidant system to re-establish the cellular redox equilibrium and homeostasis (Valliyondan and Nguyen 2006; Munns and Tester 2008). Heat stress changes the expression of gene at molecular level (Shinozaki and Yamaguchi-Shinozaki 2007; Collins et al. 2008). Osmoprotectants, detoxifying enzymes, transporters and regulatory proteins controlled gene expression is depend upon heat stress condition (Semenov and Halford 2009; Krasensky and Jonak 2012). Heat stress depends upon three factor and they are duration of temperature, degree of temperature and nature of crop. To survival and growth of plant in heat stress condition one mechanisms activated which lead to cellular dead or injury within few minutes which responsible for catastrophic collapse of cellular organization (Ahuja et al. 2010). Different plant stages such as germination, growth, development, fertilization and reproduction influence by heat stress (Mittler and Blumward 2010). High temperature stress differentially affect the protein stability, membrane, RNA species and structure of cytoskeleton and alters the efficiency of enzymatic reaction in the cell for which responsible for alter and imbalance metabolic and physiological process (Ruelland and Zachowski 2010). Heat stress responsible for loss of cell water content due to that cell size and growth is decreases (Rodriguez et al. 2005). Relative growth rate (PGR) in maize and millet reduced due to reduction in net assimilation rate (NAR) under heat stress (Wahid 2007). Leaf firing tassel blast, leaf senescence, inhibition of root and shoot, changes color of fruit and damage sign in fruit were important morphological sign under heat stress condition (Rodriguez et al. 2005).

Heat stress causes reduction of plant growth duration due to increases growth rate and ultimate shorter life cycle of crop. Temperature ( $>1-2^\circ\text{C}$ ) than the normal lead to reduction in grain filling duration and negatively affect yield and yield attributing traits (Zhang et al. 2006). Plant growth and development stages are susceptible to heat stress. In comparison to vegetative stages of crop reproductive stage is most susceptible to heat stress and few degrees increases in temperature at the time of flowering causes entire loss of grain cycle (Lobell et al. 2011). Plant species showed significant variation in decreases in floral bud and flower abortion under heat stress conditions (Demirevskya-kepova et al. 2005). In Heat stress conditions leads to impaired cell division in both male and female organs, pollen tube germination and growth, ovule viability, anomaly in position of stigmatic and style, number of pollen per silk during fertilization, poor growth endosperm, pro-embryo and barren embryo. These mechanisms are

also responsible for production of sterile plant due to absent in flower or fruit at reproductive stage (Yun-Ying et al. 2008). Under stressful environmental condition genetic improvement can be achieved by selection of primary traits such as yield and secondary trait related to improved yield potential secondary traits more important for genetic improvement for maize population under abiotic stress condition (Betran et al. 2003).

#### **Anthesis –silking interval (ASI)**

Chapman et al. (1997b) reported that most of high yielding plant in most of environment had short ASI and Higher ear per plant (EPP) particularly in drought environments. Boonpradub and Senthong (2001) reported that ASI was negatively correlated with kernel yield only for dry regime. Betran et al. (2003a) reported that shorter ASI were associated with higher grain yields. Difference in grain yield under drought imposed were strongly associated with reduces ASI. When high difference between anthesis and tassing in maize leads to responsible for longer anthesis silking interval under high temperature condition (Cicchino et al. 2010).

#### **Tassel blast**

Tassel blast was found to be negatively and highly significantly correlated with grain yield and positive significant association between leaf firing in maize (Hussain et al. 2006).

#### **Leaf firing**

Chen et al. (2010) reported that under high temperature stress condition leaf firing reduces photosynthetic apparatus. Significant reduction in yield per plant with increase in percent leaf firing and days to flowering and reduction in chlorophyll fluorescence and number of tassel branches in heat stress were also reported by Bai (2003).

#### **Silk receptivity (%)**

Kernel number per cob was control by number of pollen available at time of silking in maize. Pollen densities less than 3000 pollen grain per silk required for optimum number of kernel production in maize. So minimum number of pollen density per exposed silk is required for maximum grain yield (Westgate et al. 2003). Maize kernel set determine by silk elongation pattern and duration of silk receptivity. Silk elongation and senescence variation lead to determine grain yield (Anderson et al. 2004). Campos et al. (2004) reported that grain yield performance in multi environmental condition under drought condition trough increase yield potential and kernel set rapid silk exertion and reduced barrenness through at lower rate than under optimal condition help the selection heat stress tolerance genotypes in heat stress breeding.

#### **Leaf senescence (%)**

Lobell et al. (2012) reported senescence as limiting factor for grain filling and grain yields under heat stress. Kamara et al. (2003) concluded leaf dead score did not significantly correlated with grain yield but were highly correlated with LAI indicating the importance of green area for which is related to chlorophyll content and responsible for photosynthesis and help in maintains of high grain yield under drought. Delayed senescence which means stay green nature of plant is secondary character importance and relatively high leaf chlorophyll during late grain filling in stress (Zaidi et al. 2004).

#### **Crop maturity days**

Grain filling duration time between heading date to physiological maturity and rate no significant association with grain yield in most of cases. But under water deficient condition during maturities it was associated with increases yield in cereals (Talbert et al. 2001).

#### **Chlorophyll content**

Grain yield was significantly correlated with chlorophyll content and EPP under severe drought stress condition (Betran et al. 2003a). The association between leaf injury and low chlorophyll content in maize plants (Liu and Huang 2000).

#### **Plant height**

Reduction of rate of growth of first internode of plan under the heat stress condition which initial step of plant height development in maize and that determine plant height in maturity (Weaich et al. 1996).

#### **Number of kernel per ear**

Under heat stress condition in corn kernel number loss due to kernel abortion due to pollen viability and pollination dynamics which ultimate limit the crop production (Cicchino et al. 2010b).

#### **Grain yield**

Maize inbred lines reduced grain yield up to 70% in high temperature condition (Khodarahmpour et al. 2011). Lower grain yield was associated with pollen viability and fertilization under high temperature (Rowhani et al. 2011). Grain filling as one of most sensitive stage of corn under heat stress (Thompson 1986). Grain yield and biomass production was affects by heat stress but mechanism was varying with crop stage. Stress in pre-anthesis stress leading to barrenness in plants, while absorption of fertilized structure and reduced ear growth rate lead to reduction in kernel number and ultimate affect crop yield (Cicchino et al. 2010b).

### Genetic constitution and regulation of heat stress tolerance

Maize kernel contains about 80 % endosperm and 20 embryos. DNA endo-duplication observed in maize (Kowles and Phillips 1985). It involved in increase gene expression for kernel filling and kernel fresh weight (Kowles et al. 1992). Thus endo-duplication, nuclear DNA and fresh weight reduce with increase in temperature (Engelen-Eigles et al. 2000). Hence, conferring stability of endo-reduplication under heat stress must be an important criterion for optimizing crop yields in maize. Under heat stress condition reduces the synthesis of photosynthetic apparatus RUBISCO and PEPC and zein protein (Monjardino et al. 2006) which means post transcriptional response in maize. A number of genes occurring in response to various stresses at the transcriptional level have been reported for controlling physiological and biochemical changes (Yamaguchi-Shinozaki and Shinozaki 2006). Among these, transcription factors play a crucial role. These transcription factors bind to an element sequence in the promoter region and activate the expression of downstream genes involved in abiotic stress response. Up-regulation of genes for synthesis of protein that mitigate the effect of temperature stress has also been reported in maize in response to high temperature hocks (Qin et al. 2007). Inductions of these heat inducible genes are leads to the binding of heat shock factors to a conserved heat-shock element (HSE) in the promoter region of the genes.

#### Maize endosperm Adp-Glucose Pyrophosphorylase (AGP)

Starch accounts for nearly 70 % of maize kernel and its synthesis pathway affects the heat stress (Greene and Hanah 1998). Under heat stress conditions some AGP enzyme doesn't work. A point mutation in the *Shrunken2* (*Sh2*) gene encoding for the larger subunit of AGP and it enhanced interaction of subunit for increases maize endosperm AGP stability (Greene and Hannah 1998). Maize endosperm AGP (*Sh2hs33*) help for changes in flux of carbon into starch in maize kernels, thus, play significant role in minimum loss of grain yield at heat stress condition. Studies have also shown enhanced heat stability of AGP by insertion of a cysteine in the N- terminus of the small subunit has been reported to provide a 70-fold increase in heat stability at 55°C encoded by *Brittle2* gene (Linebarger et al. 2005).

#### Maize catalase activity

Elevated temperatures above normal condition in maize crop leads to reduce the scutellar catalase activity. The decline in Catalase activity leads decreases levels of the *Cat2* transcript which responsible for reduction in production *CAT-2* isozyme. Trans-acting gene locus *Car1* regulated

*CAT-2* activity levels and in heat stress condition it is possible that *Car1* gene product is inhibited. Thus accumulation or stability of *Cat1* mRNA with high temperature condition indicate that *CAT-1* play significant role in development of thermo-tolerant maize by its protective role as well as compensate in the absence of other catalases.

#### Heat Shock Proteins (HSPs)

Maize synthesized a few novel protein termed heat shock proteins and it acting as molecular a chaperone, stabilizing other proteins in a particular state of folding and preventive stress-induced denaturation and aggregation. Maize male reproductive part such as pollen have initial synthesis HSPs during its production stage while when it goes maturation it losses it synthesized capacity and became heat susceptible in comparison to female tissues able to synthesis HSPs at any growth stage this indicated that pollen more susceptible to heat stress in comparison to silk (Dupuis and Dumans 1990). Among different stage of pollen development late microspore (vacuolated), late bicellular pollen, early tricellular pollen, mid tricellular pollen and mature pollen exhibit HSP70 protein at initial stage of pollen development which was found much small amount than in vegetative tissues of crop which were regulated by *hsp 70* genes (Gagliardi et al. 1995). Mid-tricellular and mature pollen stages losses its HSPs response and stop the accumulation of HSP70 transcripts (Hopf et al. 1992). It was found that HSP60, HSP70, HSP90, HSP101 were major classes of HSPs and play role in protection of maize under heat stress condition. Lund et al. (1998) suggested that Mitochondrial HSP22 play role in protection as organellar signaling of mitochondria during heat stress in maize. A nucleus- localized Hsp 101 protein provides and maintenance the more thermo tolerant capacity in germinating maize kernels as well as it play negative role in primary root growth as cellular roles (Nieto-Sotelo et al. 2002). Hsp101 accumulates in fully mature and germinating kernels of maize even in the absence of high temperature stress and it is found in embryo axis and scutellar region and its level decreases 3 days after imbibition (Nieto-Sotelo et al. 2002). Thus HSP101 play role in development of heat stress tolerant genotypes due to less reduction in number of kernel per ear under heat stress condition. In young male inflorescence contains pollen grains which contained high amount of Hsp101 protein at initial stage of pollen development while when it goes its maturation time it loses Hsp 101 protein activity and become heat susceptible at time of anthesis period (Young et al. 2001). Ear increases Hsp101 level during its early development as well as silk present in ear also contained similar amount of this protein both prior to and up to 1 week

following fertilization. Ear increases level of Hsp101 under high temperature condition and its expression in the endosperm and embryo is not responsive to heat stress condition. Maize chromosome 6 consisted up Hsp 101 protein coded gene and this location was closely connected with umc 132 and npi 280 two genetic marker at QTL analysis and which are already found to be associated with some thermo tolerant traits and yield attributing traits (Sanguineti et al. 1999). The normal growth and development of plant is not affecting by HSP101 protein over and under expression. Thus expression of HSP101 help to increases plant capacity to survival under heat stress condition in plant (Queitsch et al. 2000). Thus expression of HSP101 in heat sensitive tissue and different development stage of plant as one of attractive target for improving heat stress tolerance in plants. Thus HSP101 expression at pollen tissue at high temperature might help in grain yield improvement due to increases fertilization capacity at time of heat stress condition (Gurley 2000).

#### **Maize chloroplast protein synthesis elongation factor (EF-TU)**

Maize chloroplast protein synthesis elongation factor (EF-Tu) play important role for protection of crop from high temperature condition (Ristic et al. 1998; Bhadula et al. 2001). It behaves as molecular chaperone and chloroplast protein protection from aggregation and inactivation in high temperature condition (Rao et al. 2004; Ristic et al. 2004). These are produced in cytosol and brought in the chloroplasts and likely of nuclear origin. Granal chloroplasts consist relative lower level of this protein in comparison to agranal chloroplasts and under normal condition it is found in stoma (Momcilovic and Ristic 2004). Momcilovic and Ristic (2007) reported plant different stages exhibited different expression and control in chloroplast EF-Tu and regulation of expression of EF-Tu genes varies in the heat sensitive and tolerant lines of maize crop. Plant production of EF-Tu transcript and EF-Tu protein in all age means this protein help regulation and control heat stress condition in maize for development of thermo tolerant nature where in comparatively lower thermo tolerance genotype showed that increases accumulation of EF-Tu up to 14 days of age under high temperature condition then after level of production of EF-Tu mRNA, was slow as well as not preceded, which showed EF-Tu synthesis process is control by post-transcriptional level. Chloroplast protein synthesis elongation factor (EF-Tu) in maize has also shown genetic evidence for association with heat tolerance and has been found to segregate in Mendelian fashion. Thus from this study this heat shock EF-Tu protein can play significant role in production of thermo-tolerance plant which control by post-

transcriptional level with help different tools of plant breeding such as genetically engineered and significant role in stabilizing crop yield in heat stress conditions (Ristic et al. 2004).

#### **CONCLUSIONS**

High temperature stress greatly affects the growth, development, and productivity of maize plants. It brings changes in morphology, plant physiology and molecular level of plants. The plant responses to elevated temperatures, and the mechanisms underlying the development of heat-tolerance, need to be better understood for development of heat stress tolerant varieties. The responses of plants to heat stress have been studied intensively in recent years; however, a complete understanding of thermotolerance mechanisms remains elusive. Field experiments should be conducted to identify different biochemical and molecular approaches and agronomic management practices which are needed to investigate the actual high temperature stress responses and their effects on final crop yield.

#### **REFERENCES**

- Ahn Y. J. Zimmerman J. (2006) Introduction of the carrot HSP17.7 into potato (*Solanum tuberosum L.*) enhances cellular membrane stability and tuberization in vitro. *Plant, Cell and Environment*, 29(1): 95-104.
- Ahuja I. deVos R. C. Bones A. M. Hall R. D. (2010) Plant molecular stress responses face climate change. *Trends in Plant Science*, 15(12): 664-674.
- Akbar M. Saleem M. Ashraf M. Y. Husain A. Azhar F. M. Ahmad R. (2009) Combining ability studies for physiological and grain yield traits in maize at two temperature regimes. *Pakistan Journal of Botany*, 41(4): 1817-1829.
- Akbar M. Saleem M. Azhar F. M. Ashraf M. Y. Ahmad R. (2008) Combining ability analysis in maize under normal and high temperature conditions. *Journal of Agricultural Research*, 46(1): 261-277.
- Anderson S. R. Lauer M. J. Schoper J. B. Shibles R. M. (2004) Pollination timing effects on kernel set and silk receptivity in four maize hybrids. *Crop Science*, 44(2): 464-473.
- Bai J. (2003) Genetic variation of heat tolerance and correlation with other agronomic traits in a maize (*Zea mays L.*) recombinant inbred line population (Doctoral dissertation, Texas Tech University). PP. 1-91
- Betrán F. J. Beck, D. Bänziger M. Edmeades G. O. (2003a) Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize. *Field Crops Research*, 83(1): 51-65.

- Bhadula S. K. Elthon, T. E. Habben J. E. Helentjaris T. G. Jiao S. Ristic Z. (2001) Heat-stress induced synthesis of chloroplast protein synthesis elongation factor (EF-Tu) in a heat-tolerant maize line. *Planta*, 212 (3); 359-366.
- Boonpradub S. Senthong C. (2001) Drought response of maize genotypes under an irrigation gradient. *Thai Journal of Agricultural Science (Thailand)*, 34(3-4): 217-228.
- Camejo D. Rodríguez P. Morales M. A. Dell'Amico J. M. Torrecillas A. Alarcón J. J. (2005) High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *Journal of Plant Physiology*, 162(3): 281-289.
- Campos H. Cooper M. Habben J. E. Edmeades G. O. Schussler J. R. (2004) Improving drought tolerance in maize: a view from industry. *Field Crops Research*, 90(1): 19-34.
- Chapman S. C. Crossa J. Basford K. E. Kroonenberg P. M. (1997) Genotype by environment effects and selection for drought tolerance in tropical maize. II. Three-mode pattern analysis. *Euphytica*, 95(1): 11-20.
- Chen J. Xu W. Burke J. J. Xin Z. (2010) Role of phosphatidic acid in high temperature tolerance in maize. *Crop Science*, 50(6): 2506-2515.
- Chen Y. Burris J. S. (1990) Role of carbohydrates in desiccation tolerance and membrane behavior in maturing maize seed. *Crop Science*, 30(5): 971-975.
- Cicchino M. Edreira J. I. Otegui M. E. (2010b) Heat stress during late vegetative growth of maize: effects on phenology and assessment of optimum temperature. *Crop Science*, 50(4): 1431-1437.
- Cicchino M. Edreira J. I. Uribealarea M. Otegui M. E. (2010a) Heat stress in field-grown maize: Response of physiological determinants of grain yield. *Crop Science*, 50(4): 1438-1448.
- Collins N. C. Tardieu F. Tuberosa, R. (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand. *Plant Physiology*, 147(2): 469-486.
- Demirevska-Kepova K. Holzer R. Simova-Stoilova L. Feller U. (2005) Heat stress effects on ribulose-1, 5-bisphosphate carboxylase/oxygenase, Rubisco binding protein and Rubiscoactivase in wheat leaves. *Biologia Plantarum*, 49(4): 521-525.
- Dupuis I. Dumas C. (1990) Influence of temperature stress on in vitro fertilization and heat shock protein synthesis in maize (*Zea mays L.*) reproductive tissues. *Plant Physiology*, 94(2): 665-670.
- Engelen-Eigles G. Jones R. J. Phillips R. L. (2000) DNA endoreduplication in maize endosperm cells: the effect of exposure to short-term high temperature. *Plant, Cell and Environment*, 23(6): 657-663.
- Feder M. E. Hofmann G. E. (1999) Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annual Review of Physiology*, 61(1): 243-282.
- Gagliardi D. Breton C. Chaboud A. Vergne P. Dumas C. (1995) Expression of heat shock factor and heat shock protein 70 genes during maize pollen development. *Plant Molecular Biology*, 29(4): 841-856.
- Greene T. W. Hannah L. C. (1998) Enhanced stability of maize endosperm ADP-glucose pyrophosphorylase is gained through mutants that alter subunit interactions. *Proceedings of the National Academy of Sciences*, 95(22): 13342-13347.
- Gurley W. B. (2000) HSP101: a key component for the acquisition of thermotolerance in plants. *The Plant Cell*, 12(4): 457-460.
- Hasanuzzaman M. Nahar K. Fujita M. (2013) Plant response to salt stress and role of exogenous protectants to mitigate salt-induced damages. In *Ecophysiology and Responses of Plants under Salt Stress* (pp. 25-87). Springer New York.
- Hopf N. Plesofsky-Vig N. Brambl R. (1992) The heat shock response of pollen and other tissues of maize. *Plant Molecular Biology*, 19(4): 623-630.
- Hussain T. Khan I. A. Malik, M. A. Ali Z. (2006) Breeding potential for high temperature tolerance in corn (*Zea mays L.*). *Pakistan Journal of Botany*, 38(4): 1185.
- Iba K. (2002) Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. *Annual Review of Plant Biology*, 53(1): 225-245.
- Kamara A. Y. Menkir A. Badu-Apraku, B. Ibikunle, O. (2003) Reproductive and stay-green trait responses of maize hybrids, improved open-pollinated varieties and farmers's local varieties to terminal drought stress. *Maydica*, 48(1): 29-38.
- Khodarahmpour Z. Choukan R. (2011) Genetic Variation of Maize (*Zea mays L.*) Inbred Lines in Heat Stress Condition. *Seed and Plant Improvement Journal*, 27(4): 539-554.
- Kowles R. V. Phillips R. L. (1985) DNA amplification patterns in maize endosperm nuclei during kernel development. *Proceedings of the National Academy of Sciences*, 82(20): 7010-7014.
- Kowles R. V. Yerk, G. L. Srienc F. Phillips R. L. (1992) Maize endosperm tissue as an endoreduplication system. In *Genetic Engineering* (pp. 65-88). Springer US.
- Krasensky J. Jonak C. (2012) Drought, salt, and temperature stress-induced metabolic

- rearrangements and regulatory networks. *Journal of Experimental Botany*, 63(4): 1593-1608.
- Linebarger C. R. L. Boehlein S. K. Sewell A. K. Shaw J. Hannah L. C. (2005) Heat stability of maize endosperm ADP-glucose pyrophosphorylase is enhanced by insertion of a cysteine in the N terminus of the small subunit. *Plant Physiology*, 139(4): 1625-1634.
- Liu, X. Huang B. (2000) Heat stress injury in relation to membrane lipid peroxidation in creeping bentgrass. *Crop Science*, 40(2): 503-510.
- Lobell D. B. Schlenker W. Costa-Roberts J. (2011) Climate trends and global crop production since 1980. *Science*, 333(6042): 616-620.
- Lobell D. B. Sibley A. Ortiz-Monasterio J. I. (2012) Extreme heat effects on wheat senescence in India. *Nature Climate Change*, 2(3):186-189.
- Lund A. A. Blum P. H. Bhattaramakki, D. Elthon, T. E. (1998) Heat-stress response of maize mitochondria. *Plant Physiology*, 116(3): 1097-1110.
- Mittler R. Blumwald E. (2010) Genetic engineering for modern agriculture: challenges and perspectives. *Annual Review of Plant Biology*, 61: 443-462.
- Momcilovic I. Ristic Z. (2004) Localization and abundance of chloroplast protein synthesis elongation factor (EF-Tu) and heat stability of chloroplast stromal proteins in maize. *Plant Science*, 166(1): 81-88.
- Momcilovic I. Ristic Z. (2007) Expression of chloroplast protein synthesis elongation factor, EF-Tu, in two lines of maize with contrasting tolerance to heat stress during early stages of plant development. *Journal of Plant Physiology*, 164(1): 90-99.
- Monjardino P. Smith A. G. Jones R. J. (2006) Zein transcription and endoreduplication in maize endosperm are differentially affected by heat stress. *Crop Science*, 46(6): 2581-2589.
- Munns R. Tester M. (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 59: 651-681.
- Nieto-Sotelo J. Martínez, L. M. Ponce, G. Cassab G. I. Alagón, A. Meeley R. B. Yang R. (2002) Maize HSP101 plays important roles in both induced and basal thermo tolerance and primary root growth. *The Plant Cell*, 14(7): 1621-1633.
- Qin F. Kakimoto M. Sakuma Y. Maruyama K. Osakabe Y. Tran L. S. P. Yamaguchi-Shinozaki K. (2007) Regulation and functional analysis of ZmDREB2A in response to drought and heat stresses in *Zea mays* L. *The Plant Journal*, 50(1): 54-69.
- Queitsch C. Hong S. W. Vierling E., Lindquist S. (2000) Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis. *The Plant Cell*, 12(4):479-492.
- Rao D. Momcilovic I. Kobayashi S. Callegari E. Ristic Z. (2004) Chaperone activity of recombinant maize chloroplast protein synthesis elongation factor, EF-Tu. *European Journal of Biochemistry*, 271(18): 3684-3692.
- Ristic Z. Wilson K. Nelsen C. Momcilovic I. Kobayashi S. Meeley R. Habben J. (2004) A maize mutant with decreased capacity to accumulate chloroplast protein synthesis elongation factor (EF-Tu) displays reduced tolerance to heat stress. *Plant Science*, 167(6): 1367-1374.
- Ristic Z. Yang G. Martin B. Fullerton S. (1998) Evidence of association between specific heat-shock protein (s) and the drought and heat tolerance phenotype in maize. *Journal of Plant Physiology*, 153(3): 497-505.
- Rodríguez M. Canales E. Borrás-Hidalgo O. (2005) Molecular aspects of abiotic stress in plants. *Biotechnología Aplicada*, 22(1): 1-10.
- Rowhani P. Lobell D. B. Linderman M. Ramankutty N. (2011) Climate variability and crop production in Tanzania. *Agricultural and Forest Meteorology*, 151(4): 449-460.
- Ruelland E. Zachowski A. (2010) How plants sense temperature. *Environmental and Experimental Botany*, 69(3): 225-232.
- Sanguineti M. C. Tuberosa R. Landi P. Salvi S. Maccaferri M. Casarini E. Conti S. (1999) QTL analysis of drought-related traits and grain yield in relation to genetic variation for leaf abscisic acid concentration in field-grown maize. *Journal of Experimental Botany*, 50(337): 1289-129.
- Semenov M. A. Halford N. G. (2009) Identifying target traits and molecular mechanisms for wheat breeding under a changing climate. *Journal of Experimental Botany*, 60(10): 2791-2804.
- Shinozaki K. Yamaguchi-Shinozaki K. (2007) Gene networks involved in drought stress response and tolerance. *Journal of Experimental Botany*, 58(2): 221-227
- Talbert L. E. Lanning S. P. Murphy R. L. Martin J. M. (2001) Grain fill duration in twelve hard red spring wheat crosses. *Crop Science*, 41(5): 1390-1395.
- Tassawar H. Iftikhar A. K. Zulfiqar A. (2012) Study on gene action and combining abilities for thermotolerant abilities of corn (*Zea mays* L.). *International Journal of Plant Production*, 1(1): 1-12.
- Thompson L. M. (1986) Climatic change, weather variability, and corn production. *Agronomy Journal*, 78(4):649-653.
- Valliyodan B. Nguyen H. T. (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in

- plants. *Current opinion in Plant Biology*, 9(2): 189-195.
- Wahid A. Gelani S. Ashraf M. Foolad M. R. (2007) Heat tolerance in plants: an overview. *Environmental and Experimental botany*, 61(3): 199-223.
- Wang J. Z. Cui L. J. Wang Y. Li J. L. (2009) Growth, lipid peroxidation and photosynthesis in two tall fescue cultivars differing in heat tolerance. *Biologia Plantarum*, 53(2): 237-242.
- Weaich K. Bristow K. L. Cass A. (1996) Modeling preemergent maize shoot growth: II. High temperature stress conditions. *Agronomy Journal*, 88(3): 398-403.
- Westgate M. E. Lizaso J. Batchelor W. (2003) Quantitative relationships between pollen shed density and grain yield in maize. *Crop Science*, 43(3): 934-942.
- Yamaguchi-Shinozaki K. Shinozaki K. (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology*, 57: 781-803.
- Yamamoto K. Sakamoto H. Momonoki Y. S. (2011) Maize acetylcholinesterase is a positive regulator of heat tolerance in plants. *Journal of plant physiology*, 168(16): 1987-1992.
- Young T. E. Ling J. Geisler-Lee C. J. Tanguay R. L. Caldwell C. Gallie D. R. (2001) Developmental and thermal regulation of the maize heat shock protein, HSP101. *Plant Physiology*, 127(3):777-791.
- Yun-Ying C. A. O. Hua, D. Li-Nian Y. A. N. G. Zhi-Qing W. A. N. G. Shao-Chuan Z. H. O. U. Jian-Chang Y. A. N. G. (2008) Effect of heat stress during meiosis on grain yield of rice cultivars differing in heat tolerance and its physiological mechanism. *Acta Agronomica Sinica*, 34(12): 2134-2142.
- Zaidi P. H. Srinivasan G. Cordova H. S. Sanchez C. (2004) Gains from improvement for mid-season drought tolerance in tropical maize (*Zea mays L.*). *Field Crops Research*, 89(1): 135-152.
- Zhang Y. Mian M. A. R. Bouton J. H. (2006) Recent molecular and genomic studies on stress tolerance of forage and turf grasses. *Crop Science*, 46(2): 497-511.