Chapter

Breeding Mechanisms for High Temperature Tolerance in Crop Plants

Priyanka Shanmugavel, Sudhagar Rajaprakasam, Vanniarajan Chockalingam, Gowtham Ramasamy, Kalaimagal Thiyagarajan and Rajavel Marimuthu

Abstract

Increase in global warming poses a severe threat on agricultural production thereby affecting food security. A drastic reduction in yield at elevated temperature is a resultant of several agro-morphological, physiological and biochemical modifications in plants. Heat tolerance is a complex mechanism under polygenic inheritance. Development of tolerant genotypes suited to heat extremes will be more advantageous to tropical and sub tropical regimes. A clear understanding on heat tolerance mechanism is needed for bringing trait based improvement in a crop species. Heat tolerance is often correlated with undesirable traits which limits the economic yield. In addition, high environmental interactions coupled with poor phenotyping techniques limit the progress of breeding programme. Recent advances in molecular technique led to precise introgression of thermo-tolerant genes into elite genetic background which has been reviewed briefly in this chapter.

Keywords: global warming, high temperature, polygenic inheritance, breeding approaches, thermo-tolerant genes

1. Introduction

Increase in global temperature had major impact on crop productivity especially in tropical and sub tropical regimes. Based on climate model predictions, around 1.8–4.0°C rise in air temperature was expected in 21st century [1]. The increase in temperature beyond a certain threshold level tends to induce detrimental effects in plant growth and development. In general, the elevation in temperature of 10–15°C above ambient triggers heat shock in crop plants. The extent of induced heat stress depends on the duration, intensity and rate of increase in global air temperature [2]. Indian lowlands share 15 per cent of global wheat production. The change in global climate would shift these fertile lowlands into heat stressed unproductive environment [3]. Similarly, the cultivation of cereals in Southern Africa and South East Asia was predicted to be heat stressed zone in near future [4]. Around 4–14% yield decline in rice was encountered due to elevated temperature of 1°C in South-East Asia [5]. The declined productivity due to elevated temperature imposes the urgent need for development of climate resilience genotypes. Evolving heat tolerant cultivars would highly benefit the livelihood of developing countries as around 70–80% of population relies on agriculture. Understanding the effect of heat stress on crop plants and its adaptation mechanisms would help in framing out the breeding strategies for high temperature tolerance.

Heat tolerance in crop plants is a complex mechanism involving adaptations through altered physiological process, morpho-anatomical features and induction of several biochemical pathways. On exposure to high temperature, several signal transduction pathways were triggered leading to changes in gene expression. As a result, varied stress related proteins were synthesized contributing heat tolerance in plants [6]. The tolerance mechanism to high temperature stress varies within genotypes of a plant species. The existing variation between and within species provide scope for evolving heat tolerant lines through conventional breeding approaches [7]. Dissecting out genetic information through molecular tools would hasten the development of climate resilient cultivars contributing to food security in near future. A brief review on plant response, adaptation mechanisms and genetic approaches to combat heat stress were presented in this chapter.

2. Effect of heat stress on crop plants

Heat stress had varying impact on different phenological stages *viz*., germination, seedling, vegetative, flowering and reproductive of crop plants [8]. The plant response to heat stress depends on the duration, degree of rise in temperature and plant type. Under tropical regimes, high temperature with intense solar radiation poses a major limiting factor for yield by inducing leaf abscission, leaf senescence, scorching of leaves, branches and stems, growth inhibition, pollen infertility and poor seed formation [9, 10]. A significant decline in relative growth rate, shoot dry weight and net assimilation rate was recorded in sugarcane, maize and pearl millet on exposure to high temperature stress [11]. High reduction in grain quality was recorded in most of the cereal crops grown under heat stress environments [12]. Several physiological processes such as partitioning of assimilates, plant-water relations and shoot growth was affected due to heat stress in common bean [13]. In general, the susceptibility to heat stress was found higher at reproductive stage of plant development. An excessive yield loss is recorded in legumes on exposure to high temperature (30–35°C) during anthesis stage [14]. Drastic reduction in grain number and weight was observed in wheat at high temperature regimes [15]. Heat stress affects several metabolic pathways leading to accumulation of reactive oxygen species (ROS) which is a major component for oxidative stress in crop plants [16]. The photosystem centres (PS I and PS II) of chloroplast, mitochondria and peroxisomes are the major sites for generation of ROS in plants [17]. High temperature stress disrupts the stability of cell membrane through protein denaturation [18]. The induction of ROS due to high temperature stress was correlated with premature leaf senescence in *Gossypium* sp. [19]. Accumulation of ROS in root cells was evidenced in wheat on exposure to high temperature for two days [20].

3. Adaptation mechanisms

Plants tend to adapt several complex mechanisms through phenological and morphological changes to combat high temperature stress (**Figure 1**). On heat stress regimes, plants exhibit varied short term escape/avoidance mechanisms *viz*., altered leaf orientation, transpirational cooling, altered membrane lipid properties, early maturation and so on for its survival. Plants show varied degree of leaf rolling

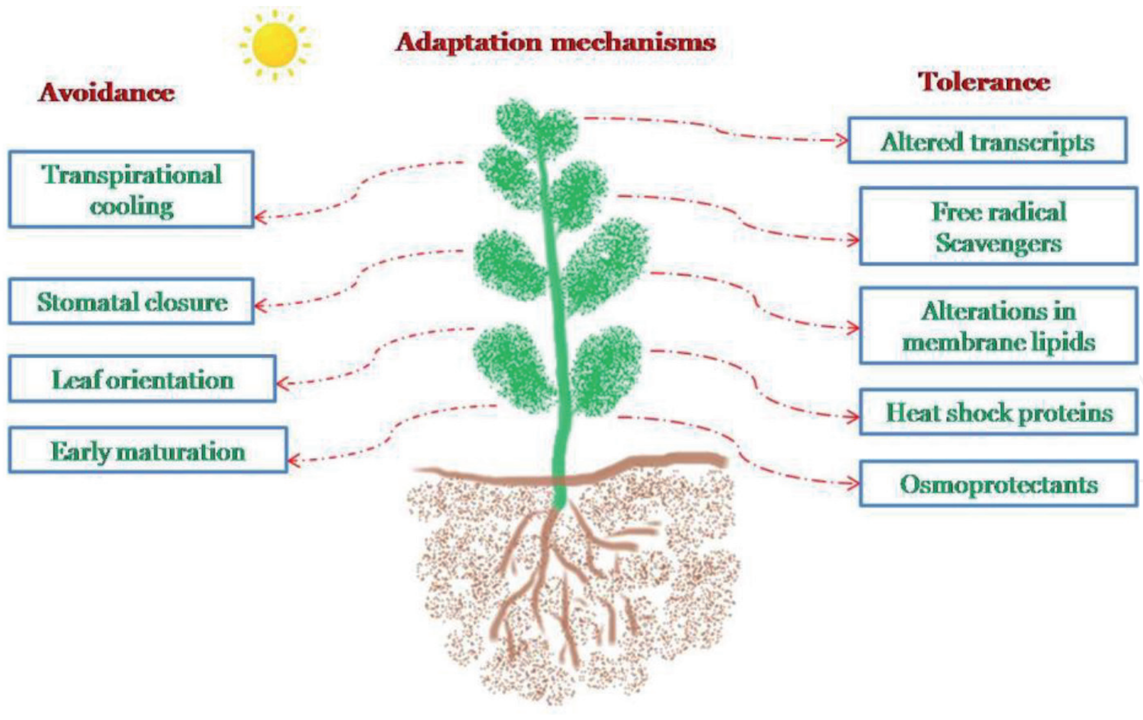

Figure 1.
Adaptation mechanisms for high temperature tolerance in crop plants.

upon intensity of solar radiation. A significant tolerance to high temperature was observed in wheat by maintenance of water potential in flag leaf through adoption of leaf rolling under heat shock conditions [21]. Increase in trichomatous and stomatal densities, waxy layer on leaves, and larger xylem vessels are the common features induced during heat stress [22]. On contrary, plants also evolve long term tolerance mechanisms for its effective survival and productivity under high temperature. Induction of osmoprotectants, antioxidants, late embryogenesis abundant proteins, dehydrins, and heat shock proteins are the major factors involved in counteracting the heat shocks. Accumulation of osmolytes such as proline, trehalose, and glycine betaine plays a vital role in imparting tolerance *via* cellular osmotic adjustment, detoxification of ROS, stabilization of enzymes and membrane proteins [23]. Several enzymatic and non-enzymatic antioxidant defense components are also involved in protection against oxidative stress induced by free radicals [24]. The activities of ROS scavenging enzymes are temperature specific. In general, most of the antioxidant enzymes show increased activity with elevation in temperatures. It is also influenced by genotype, growing season and phenological stages of plant [25]. Under high temperature conditions, several signaling molecules such as nitrous oxide, Ca-dependent protein kinases, Mitogen mediated protein kinase, sugars, and phytohormones play a role in stimulation of stress responsive genes *via* transduction pathways [26]. Evolving adaptation mechanisms (either tolerance or avoidance) to high temperature and drought would be more rewarding at arid conditions as it is often correlated.

4. Thermo-tolerance through breeding strategies

4.1 Screening criteria

Breeding for high temperature tolerance requires an essential knowledge on plant adaptation response to heat shocks. In general, the genotypes exhibiting less detrimental effect on photosynthesis and reproductive development tend to survive well under heat prone areas [27]. Involvement of these two components in selection criteria would be beneficial in evolving thermo tolerant cultivars. Tolerant genotypes evolve several morphological, physiological and biochemical alterations in response to heat shocks. Knowledge on sensitivity of several phenological stages to high temperature will pave way for trait specific improvement. High temperature is often correlated with other environmental factors which poses a major limitation for selection under field conditions. At present, varied selection criteria has been developed by scientists, which favors delineation of superior variety at prevailing environment [28]. Heat tolerant index has been evolved for sorghum which depicts the proportion of growth recovery after exposure to high temperature stress. It is the ratio of increase in coleoptile growth in a heat stress environment [50°C] to the enhancement in coleoptile length under normal environment (non-stress) [29]. It proves cost effective and rapid method to screen a large population size within shorter period. A proper validation of such technique would facilitate the development of tolerant lines in other crop species. Pollen viability and fruit set was considered as major selection criteria to predict yield under high temperature stress in tomato [30]. Physiological based trait selection such as harvest index, photosynthetic efficiency, respiration rate, delayed senescence and canopy architecture will also contribute towards increased tolerance to heat stress [31, 32].

4.2 Genetic resources for thermo tolerance

Inter-mating among closely related individuals for improvement of economic traits resulted in decline of genetic variability in a crop species [33]. Characterization of gene pool including land races and wild relatives would offer several tolerant genes for abiotic tolerance. Extensive efforts were made in screening of heat tolerant genotypes which can be directly introduced as a cultivar or utilized to introgress gene into new genetic background [34]. Thermo-tolerant lines were successfully isolated from wild gene pool in wheat [35]. High magnitude of variation was observed in wild progenitor "*Aegilops tauschii*" of wheat for cell viability and membrane stability [36]. Similarly, a heat tolerant source for reproductive stage was identified in *A. geniculata* and *A. speltoides* Tausch which would pave way in development of thermo-tolerant hexaploid wheat cultivars in near future [37]. A higher growth rate and improved photosynthetic efficiency was observed in wild relative "*Oryza meridionalis*" of rice at high temperature [38]. Indirect selection on pollen viability led to identification of thermo-tolerant accessions in soybean (DG 5630RR) [39], chickpea (ICC15614 & ICC1205) [40], maize (AZ100) [41], and several other crop species. Direct selection based on yield under target environment (heat stress) resulted in development of tolerant lines in many tropical grain legumes. Four tolerant genotypes/accessions *viz*., SRC-1-12-1-48, SRC-1-12-1-182, 98012-3-1-2-1 and 98020-3-1-7-2 were isolated in common bean by employing stress tolerant indices [42]. Nine thermo-tolerant wild accessions were delineated in USDA upland cotton germplasm by employing chlorophyll fluorescence technique [43].

4.3 Conventional breeding approaches

Evolving thermo-tolerance through conventional breeding approach proves promising in many crop species. Breeding for early maturing genotype in broccoli had improved head quality by avoiding heat stress at flowering stage [44]. In general, breeding programmes are carried out in hotter regions which promote selection of thermo-tolerant traits. Physiological based trait breeding was practiced at International Maize and Wheat Improvement Center (CIMMYT) for development of heat tolerant cultivars in wheat. The parental genotypes were characterized through various crossing schemes and appropriate breeding programme was framed for improvement of thermo related traits [45]. A wild ancestor "*T. tauschii*" was utilized as a gene donor for achieving increased grain size and filling percent under high temperature through recurrent selection [46]. Similarly, three cycles of recurrent selection had led to improved yield under heat stress regimes in potato [47]. Thermo tolerant alleles were introgressed into heat sensitive cultivar "Paymaster 404" from a donor accession "7456" of *G. barbadense* through backcross breeding [48]. A significant improvement in yield was realized under heat stress environment by adoption of gametic selection in maize [41]. A deep rooted cultivar "Nagina 22 (N22)" of aus rice exhibited high pollen viability and spikelet fertility (64–86%) under heat stress [49]. The thermo-tolerance of N22 was successfully introgressed into Xieqingzao B line through backcross method [50]. Dissecting out the genetic and physiological basis of thermo-tolerance will hasten up the development of resilient cultivars suited to hotter regions.

4.4 Advanced breeding approaches for thermo tolerance

The genetic basis of thermo-tolerance is not clearly understood because of complex trait inheritance. Advances in molecular approaches such as DNA marker identification and genotyping assay had paved way in determination of several QTL's associated with high temperature tolerance [51]. In wheat, QTL's were identified for canopy temperature, and chlorophyll fluorescence imparting tolerance to heat stress [52]. A major QTL "Htg 6.1" in lettuce was involved in enhancement of seed germination capacity at high temperature [53]. A recessive QTL for increased spikelet fertility under high temperature was dissected out in rice at chromosome 4. The identified QTL were found in several populations of heat tolerant rice cultivars [54]. Six QTL's were involved to enhance fruit set at high temperature in tomato [55]. Five thermo tolerant QTL's were identified in *Brassica campestris* by employing random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) markers [56]. In maize, eleven major QTL's for increased pollen germination and pollen tube growth under high temperature was mapped using restriction fragment length polymorphism (RFLP) markers [57]. Identification of candidate QTL's would pave way in precise introgression of heat tolerant genes into superior cultivars through marker assisted breeding approach.

The closely associated markers with targeted QTL will hasten the recovery of superior genotypes with heat tolerant traits in a population. A marker assisted breeding approach was employed in rice to derive heat tolerant line with superior grain quality. Two flanking markers *viz*., ktIndel001 and RFT1 enclosing 1.5 Mb chromosomal region was transferred from tolerant cultivar "Kokoromachi" to Tohoku 168. Significant improvement in grain quality under high temperature was observed in the derived NIL's compared to susceptible cultivar "Tohoku 168" [58]. Fourteen SSR markers linked to heat susceptibility index of grain filling per cent and single kernel weight was identified in bread wheat which was employed in marker assisted selection (MAS) to screen genotypes for thermo tolerance [59]. Utilization of MAS approach for heat tolerance remains less efficient because of high gene x environment and epistatic interactions. The low breeding efficiency can be resolved by genomic selection (GS) approach which involves wide number of molecular markers exhibiting high genome coverage. High genetic gain is realized in GS approach due to close association between predicted and true breeding value over generations [60].

At present, transgenic approach also proves to be desirable tool for designing thermo tolerant lines *via* introgression of genes from diverse gene pools [61]. The genetic transformation was focused primarily on transcription factors, induction of heat shock proteins, molecular chaperones, osmolytes, antioxidant components and growth regulators [62]. Heat shock proteins play a primary role in imparting thermo tolerance in crop species. It is functionally associated with diverse group of molecular chaperones that is involved in restoration of degraded proteins to their native structure under high temperature. Induction of heat shock proteins through genetic manipulation was achieved in *arabidopsis* [63], maize [64], rice [65], soybean [66], and pepper [67]. The DREB gene family was also reported to impart heat tolerant response in many crop species. Over expression of ZmDREB2A in maize [68] and GmDREB2A in soybean [69] was associated with increased survival and adaptation under high temperature. Transgenic techniques were employed to alter membrane lipid properties for thermo-tolerance in crop species. High proportion of saturated fatty acid in membrane had increased tolerance under heat stress. Suppression of omega-3 fatty acid desaturase gene in chloroplast had reduced the accumulation of trieonic fatty acid in transgenic tobacco [70] and tomato [71] leading to thermo-tolerance. A significant accumulation of glycine betaine (osmolyte) was achieved in *arabidopsis* through transfer of "cod gene" from *Arthrobacter globiformis* [72]. High proportion of glycine betaine protects the PSII component by inhibiting the ROS activities under heat stress. Implementation of transgenic approaches in other crop species will accelerate the development of resilient genotypes suited to high temperature regimes.

5. Conclusions

Development of thermo-tolerant lines has to be prioritized to meet out the future climatic change coupled with food demands. Knowledge on plant response and adaptation mechanisms to heat stress is required for framing out breeding strategies. It remains a challenging task in evolving resilient genotypes suited to high temperature because of less efficient screening protocols at field conditions. The existence of low genetic variation for heat response related traits limited the progress of conventional breeding approach in many crop species. Use of molecular breeding strategies had opened up several heat tolerant related QTL's in crop species. However, still precise research work involving huge marker data is needed for attaining high breeding efficiency for thermo tolerance. Recently, the involvement of transgenic approach paved way for utilization of tolerant source from diverse gene pools. Study on induction of heat shock proteins led to increased thermo tolerance in many crop species. Similarly, other heat response related traits such as induction of antioxidant components, osmolytes, and chaperones were also included in transgenic approach for inducing heat stress tolerance. Thus, high economic yield could be realized at elevated temperature regimes with the involvement of combined breeding approaches.

Acknowledgements

The authors are highly thankful to Dr. V. Geethalakshmi, Director, Directorate of Crop Management, Tamil Nadu Agricultural University (TNAU) for her valuable suggestions towards this chapter. We also acknowledge Dr. P. Jayamani, Professor and Head, Department of Pulses, TNAU; Dr. M. Raveendran, Professor and Head, Department of Biotechnology, TNAU; and Dr. K. Ganesamurthy, Professor and Head, Department of Rice, TNAU for rendering supportive documents on high temperature tolerance.

Conflict of interest

The authors declare no conflict of interest towards this chapter.

Thanks

The authors express their gratitude to the Directorate of Crop Management for providing scientific support on high temperature tolerance.

Author details

Priyanka Shanmugavel[1*], Sudhagar Rajaprakasam[2], Vanniarajan Chockalingam[3], Gowtham Ramasamy[4], Kalaimagal Thiyagarajan[5] and Rajavel Marimuthu[6]

1 Directorate of Crop Management, Tamil Nadu Agricultural University (TNAU), Coimbatore, India

2 Sugarcane Research Station, TNAU, Vellore, India

3 Department of Plant Breeding and Genetics, AC & RI, TNAU, Madurai, India

4 Agro Climate Research Centre, TNAU, Coimbatore, India

5 Department of Millets, TNAU, Coimbatore, India

6 Water Technology Centre, TNAU, Coimbatore, India

*Address all correspondence to: priya300593@gmail.com

References

[1] Intergovernmental Panel on Climate Change (IPCC). The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 2007. Available from: http://www.cambridge.org /features/earth_environmental/climatechange/wg1.htm"/t"blank".

[2] Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environmental and Experimental Botany. 2007;**61**:199-223

[3] Bita C, Gerats T. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress tolerant crops. Frontiers in Plant Science. 2013;**4**:273

[4] Fischer R, Edmeades GO. Breeding and cereal yield progress. Crop Science. 2010;**50**:85-98. DOI: 10.2135/cropsci2009.10.0564

[5] Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL. Prioritizing climate change adaptation needs for food security in 2030. Science. 2008;**319**:607-610

[6] Iba K. Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. Annual Review of Plant Biology. 2002;**53**:225-245

[7] Camejo D, Rodríguez P, Morales MA, Dell'amico JM, Torrecillas A, Alarcon JJ. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. Journal of Plant Physiology. 2005;162:281-289.

[8] Hasanuzzaman M, Nahar K, Fujita M. Extreme temperatures, oxidative stress and antioxidant defense in plants. In: Vahdati K, Leslie C. Abiotic Stress - Plant Responses and Applications in Agriculture. ed. InTech: Rijeka, Croatia; 2013. p. 169-205.

[9] Vollenweider P, Günthardt-Goerg MS. Diagnosis of abiotic and biotic stress factors using the visible symptoms in foliage. Environmental Pollution. 2005;**137**:455-465

[10] Ismail AM, Hall AE. Reproductive stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. Crop Science. 1999;**39**:1762-1768. DOI: 10.2135/cropsci1999.3961762x

[11] Wahid A. Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane sprouts. Journal of Plant Research. 2007;**120**:219-228

[12] Maestri E, Klueva N, Perrotta C, Gulli M, Nguyen HT, Marmiroli N. Molecular genetics of heat tolerance and heat shock proteins in cereals. Plant Molecular Biology. 2002;**48**:667-681

[13] Koini MA, Alvey L, Allen T, Tilley CA, Harberd NP, Whitelam GC, et al. High temperature-mediated adaptations in plant architecture require the bHLH transcription factor PIF4. Current Biology. 2009;**19**:408-413

[14] Siddique KHM, Loss SP, Regan KL, Jettner RL. Adaptation and seed yield of cool season grain legumes in Mediterranean environments of South-Western Australia. Australian Journal of Agricultural Research. 1999;**50**:375-387

[15] Ferris R, Ellis RH, Wheeeler TR, Hadley P. Effect of high temperature stress at anthesis on grain yield and biomass of field grown crops of wheat. Annals of Botany. 1998;**34**:67-78

[16] Asada K. Production and scavenging of reactive oxygen species in

chloroplasts and their functions. Plant Physiology. 2006;**141**:391-396

[17] Soliman WS, Fujimori M, Tase K, Sugiyama SI. Oxidative stress and physiological damage under prolonged heat stress in C_3 grass *Lolium perenne*. Grassland Science. 2011;**57**:101-106

[18] Rodríguez M, Canales E, Borrás-Hidalgo O. Molecular aspects of abiotic stress in plants. Biotechnologia Applicada. 2005;**22**:1-10

[19] Young LW, Wilen RW, Bonham-Smith PC. High temperature stress of *Brassica napus* during flowering reduces micro and megagametophyte fertility, induces fruit abortion, and disrupts seed production. Journal of Experimental Botany. 2004;**55**:485-495

[20] Miller G, Schlauch K, Tam R, Cortes D, Torres MA, Shulaev V, et al. The plant NADPH oxidase RbohD mediates rapid, systemic signaling in response to diverse stimuli. Science. Signal. 2009;**2**:ra45

[21] Sarieva GE, Kenzhebaeva SS, Lichtenthaler HK. Adaptation potential of photosynthesis in wheat cultivars with a capability of leaf rolling under high temperature conditions. Russian Journal of Plant Physiology. 2010;**57**:28-36

[22] Srivastava S, Pathak AD, Gupta PS, Shrivastava AK, Srivastava AK. Hydrogen peroxide-scavenging enzymes impart tolerance to high temperature induced oxidative stress in sugarcane. Journal of Environmental Biology. 2012;**33**:657-661

[23] Verbruggen N, Hermans C. Proline accumulation in plants: a review. Amino Acids. 2008;**35**:753-759

[24] Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress and signal transduction. Annual Review of Plant Biology. 2004;**55**:373-399

[25] Almeselmani M, Deshmukh PS, Sairam RK, Kushwaha SR, Singh TP. Protective role of antioxidant enzymes under high temperature stress. Plant Science. 2006;**171**:382-388

[26] Ahmad P, Bhardwaj R, Tuteja N. Plant signaling under abiotic stress environment. In: Ahmad P, Prasad MNV. Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate Change. ed. Springer: New York,USA; 2012.p.297-324.

[27] Prasad P, Pisipati S, Mutava R, Tuinstra M. Sensitivity of grain sorghum to high temperature stress during reproductive development. Crop Science. 2008;**48**:1911-1917. DOI: 10.2135/cropsci2008.01.0036

[28] Hall AE. Breeding Cowpea for Future Climates. In: Yadav SS, Redden R, Hatfield JL, LotzeCampen H, Hall AJW. Crop Adaptation to Climate Change. ed. Hoboken: John Wiley & Sons; 2011.

[29] Young TE, Ling J, Geisler-Lee CJ, Tanguay RL, Caldwell C, Gallie DR. Developmental and thermal regulation of maize heat shock protein, HSP101. Plant Physiology. 2001;**127**: 777-791

[30] Berry SZ, Rafique-Uddin M. Effect of high temperature on fruit set in tomato cultivars and selected germplasm. HortScience. 1988;**23**:606-608

[31] Cossani CM, Reynolds MP. Physiological traits for improving heat tolerance in wheat. Plant Physiology. 2012;**160**:1710-1718

[32] Gupta PK, Balyan HS, Gahlaut V, Kulwal PL. Phenotyping, genetic dissection, and breeding for drought and heat tolerance in common wheat: status and prospects. Plant Breeding Reviews. 2012;**36**:85

[33] Gur A, Zamir D. Unused natural variation can lift yield barriers in plant breeding. PLoS Biol. 2004;**2**:1610-1615

[34] Jagadish SVK, Craufurd PQ, Wheeler TR. Phenotyping parents of mapping populations of rice for heat tolerance during anthesis. Crop Science. 2008;**48**:1140-1146

[35] Reynolds MP, Balota M, Delgado MIB, Amani I, Fischer RA. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. Functional Plant Biology. 1994;**21**:717-730

[36] Gupta S, Kaur S, Sehgal S, Sharma A, Chhuneja P, Bains NS. Genotypic variation for cellular thermo tolerance in *Aegilops tauschii* Coss., the D genome progenitor of wheat. Euphytica. 2010;**175**:373-381

[37] Pradhan GP, Prasad PVV, Fritz AK, Kirkham MB, Gill BS. High temperature tolerance in *aegilops* species and its potential transfer to wheat. Crop Science. 2012;52:292-304.

[38] Scafaro AP, Haynes PA, Atwell BJ. Physiological and molecular changes in *Oryza meridionalis* Ng, a heat-tolerant species of wild rice. Journal of Experimental Botany. 2010;**61**:191-202

[39] Salem MA, Kakani VG, Koti S, Reddy KR. Pollen based screening of soybean genotypes for high temperatures. Crop Science. 2007;**47**:219-231

[40] Devasirvatham V, Gaur P, Mallikarjuna N, Raju TN, Trethowan RM, Tan DKY. Effect of high temperature on the reproductive development of chickpea genotypes under controlled environments. Functional Plant Biology. 2012;**39**:1009-1018

[41] Petolino JF, Cowen NM, Thompson SA, Mitchell JC. Gamete selection for heat stress tolerance in maize. In: Ottaviano E. Angiosperm Pollen and Ovules. ed. Springer: Verlag, New York; 1992. p. 355-358.

[42] Porch TG. Application of stress indices for heat tolerance screening of common bean. Journal of Agronomy and Crop Science. 2006;**192**:390-394

[43] Wu T, Weaver DB, Locy RD, McElroy S, Van Santen E. Identification of vegetative heat-tolerant upland cotton (*Gossypium hirsutum* L.) germplasm utilizing chlorophyll fluorescence measurement during heat stress. Plant Breeding. 2013;**133**:250-255

[44] Farnham MW, Bjorkman T. Breeding vegetables adapted to high temperatures: a case study with broccoli. HortScience. 2011;**46**:1093-1097

[45] Reynolds M, Manes Y, Izanloo A, Langridge P. Phenotyping approaches for physiological breeding and gene discovery in wheat. Annals of Applied Biology. 2009;**155**:309-320

[46] Gororo NN, Eagles HA, Eastwood RF, Nicolas ME, Flood RG. Use of *Triticum tauschii* to improve yield of wheat in low yielding environments. Euphytica. 2002;**123**:241-254

[47] Benites FRG, Pinto CABP. Genetic gains for heat tolerance in potato in three cycles of recurrent selection. Crop Breeding and Applied Biotechnology. 2011;**11**:133-140

[48] Rodriguez-Garay B, Barrow JR. Pollen selection for heat tolerance in cotton. Crop Science. 1988;**28**:857-859

[49] Poli Y, Basava RK, Panigrahy M, Vinukonda VP, Dokula NR, Voleti SR, et al. Characterization of a Nagina22 rice mutant for heat tolerance and mapping of yield traits. Rice. 2013;**6**:36

[50] Jiang-lin L, Hong-yu Z, Xue-lian S, Ping-an Z, Ying-jin H. Identification for

heat tolerance in backcross recombinant lines and screening of backcross introgression lines with heat tolerance at milky stage in rice. Rice Science. 2011;**18**:279-286

[51] Pinto RS, Reynolds MP, Mathews KL, McIntyre CL, Olivares-Villegas JJ, Chapman SC. Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theoretical Applied Genetics. 2010;**121**:1001-1021

[52] Vijayalakshmi K, Fritz AK, Paulsen GM, Bai G, Pandravada S, Gill BS. Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. Molecular Breeding. 2010;26:163-175.

[53] Argyris J, Dahal P, Hayashi E, Still DW, Bradford KJ. Genetic variation for lettuce seed thermo inhibition is associated with temperature-sensitive expression of abscisic acid, gibberellin, and ethylene biosynthesis, metabolism, and response genes. Plant Physiology. 2008;148:926-947.

[54] Ye C, Argayoso MA, Redon ED, Sierra SN, Laza MA, Dilla CJ, et al. Mapping QTL for heat tolerance at flowering stage in rice using SNP markers. Plant Breeding. 2012;**131**:33-41

[55] Ventura G, Grilli G, Braz LT, Gertrudes E, Lemos M. QTL identification for tolerance to fruit set in tomato by fAFLP markers. Crop Breeding and Applied Biotechnology. 2007;7:234-241.

[56] Shuancang Y, Yongiian W, Xiaoying Z. Mapping and analysis QTL controlling heat tolerance in *Brassica campestris* L. ssp. Pekinensis. Acta Horticulturae Sinica. 2003;**30**:417-420

[57] Frova C, Sari-Gorla M. Quantitative trait loci (QTLs) for pollen thermotolerance detected in maize. Molecular and General Genetics. 1994;**245**:424-430

[58] Shirasawa K, Sekii T, Ogihara Y, Yamada T, Shirasawa S, Kishitani S, et al. Identification of the chromosomal region responsible for high-temperature stress tolerance during the grain filling period in rice. Molecular Breeding. 2013;**32**:223-232

[59] Sadat S, Saeid KA, Bihamta MR, Torabi S, Salekdeh SGH, Ayeneh GAL. Marker assisted selection for heat tolerance in bread wheat. World applied sciences journal. 2013;**21**:1181-1189

[60] Habier D, Fernando RL, Dekkers JCM. Genomic selection using low-density marker panels. Genetics. 2009;**182**:343-353. DOI: 10.1534 / genetics. 108. 100289

[61] Ashraf M. Inducing drought tolerance in plants: recent advances. Biotechnology Advances. 2010;**28**:169-183

[62] Grover A, Mittal D, Negi M, Lavania D. Generating high temperature tolerant transgenic plants: achievements and challenges. Plant Science. 2013;**205**:38-47

[63] Prandl R, Hinderhofer K, Eggers-Schumacher G, Schoffl F. HSF3, a new heat shock factor from *Arabidopsis thaliana*, derepresses the heat shock response and confers thermotolerance when over expressed in transgenic plants. Molecular and General Genetics. 1998;258:269-278.

[64] Nieto-Sotelo J, Martınez LM, Ponce G, Cassab GI, Alagon A, Meeley RB, et al. Maize HSP_{101} plays important roles in both induced and basal thermotolerance and primary root growth. The Plant Cell. 2002;**14**:1621-1633

[65] Katiyar-Agarwal S, Agarwal M, Grover A. Heat-tolerant basmati rice

engineered by over-expression of hsp_{101}. Plant Molecular Biology. 2003;**51**:677-686

[66] Chen XJ, Ye CJ, Lu XY, Xu MX, Li W, Zhang LM, et al. Cloning of GmHSFA1 gene and its overexpression leading to enhancement of heat tolerance in transgenic soybean. Yi Chuan=. Hereditas. 2006;**28**:1411-1420

[67] Dang FF, Wang YN, Yu L, Eulgem T, Lai Y, Liu ZQ, et al. CaWRKY40, a WRKY protein of pepper, plays an important role in the regulation of tolerance to heat stress and resistance to *Ralstonia solanacearum* infection. Plant, Cell and Environment. 2013;**36**:757-774

[68] Qin F, Kakimoto M, Sakuma Y, Maruyama K, Osakabe Y, Tran LS, et al. Regulation and functional analysis of ZmDREB2A in response to drought and heat stresses in *Zea mays* L. The Plant Journal. 2007;**50**:54-69

[69] Mizoi J, Ohori T, Moriwaki T, Kidokoro S, Todaka D, Maruyama K, et al. GmDREB2A; 2, a canonicalDEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEIN 2-type transcription factor in soybean, is post translationally regulated and mediates dehydration-responsive element-dependent gene expression. Plant Physiology. 2013;**161**:346-361

[70] Murakami Y, Tsuyama M, Kobayashi Y, Kodama H, Iba K. Trienoic fatty acids and plant tolerance of high temperature. Science. 2000;**287**:476-479

[71] Wang HS, Yu C, Tang XF, Wang LY, Dong XC, Meng QW. Antisense-mediated depletion of tomato endoplasmic reticulum omega-3 fatty acid desaturase enhances thermal tolerance. Journal of Integrative Plant Biology. 2010;**52**:568-577

[72] Alia HH, Sakamoto A, Murata N. Enhancement of the tolerance of Arabidopsis to high temperatures by genetic engineering of the synthesis of glycine betaine. The Plant Journal. 1998;**16**:155-161