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Review Article

Experimental Strategies Presenting a Holistic View Regarding Heat Stress in Plants

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Abstract

Due to anthropogenic as well as by natural factors the climate of earth is predicted to be warm by an average of 2-4 °C, at the end of the 21st Century. Emission of green house gases (GHG) from agricultural system is one of the major contributing factor in global warming. Heat stress is one of the major abiotic stresses threatening plant growth worldwide. Agricultural crops suffer in presenting their optimum yield potential due to heat stress. Heat stress causes enormous alterations in various processes within the plant system; most of them are well understood from various physiological, biochemical and molecular studies. Heat stress not only affects the morphological and phenological parameters but also the physiological and biochemical parameters like plant water relationship, photosynthesis, assimilate partitioning, hormonal changes, cell membrane stability, production of secondary plant metabolites, antioxidative metabolism, synthesis of heat shock proteins, cell signalling etc. In the advent of climate change and subsequent global warming there is an urgent need for understanding the physiological and biochemical basis of heat stress tolerance in crop plants. There has been a lot of effort worldwide in this regard to develop high temperature tolerant genotypes through transgenic intervention and genetic engineering. This paper reviews the literature supporting evidence for the morphological, phenological, physiological and biochemical effects of heat stress on several plants and different molecular approaches to develop transgenics tolerant to high temperature stress. A plethora of these kinds of plant responses are finally regulated by the genes. Hence, more biotechnological and molecular studies including genomics, proteomics, metaboliomics and the cryptomics are necessary to elucidate the processes further.

1. Introduction

Heat is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. Heat stress due to high ambient temperatures is a serious threat to crop production worldwide (Hall, 2001). Plants generally die when exposed to temperature of 50 ^{0}C or above, but some of them tolerate high temperature above the 50 ^{0}C. By the end of the 21st Century, the earth's climate is predicted to warm by an average of 2-4 °C, due to both anthropogenic and natural factors (Eitzinger et al., 2010). IRRI, Manila, Philippines (Peng et al., 2004) reports have shown that the annual mean maximum and minimum temperatures have increased by 0·35 and 1·13°C, respectively, for the period 1979-2003. This increase in temperature has exposed most of the world's crops to heat stress during some stages of their life cycle. In general, the high temperature results loss of water so that the plants experience drought stress. The photosynthesis stops above 70-72^{o}C and the protein molecules denature. The plant which resist high temperature stress exhibit high protoplasmic viscosity, maintain higher protoplasmic hydration and possess enzymes which are more stable to high temperature. Heat stress is known to decrease the rate of photosynthesis, increase the rate of respiration, causes closure of stomata, stops CO_2 capture, increases photo-respiration and decreases the stomatal conductance causing a major slow-down in transpiration (cooling process loss and internal temperature increase). High temperature stress also results in leakage of cell membrane (signals changes in protein synthesis), continued physical loss of water, starvation of plant caused by rapid use of food reserves, inefficient food use, and inability to utilize the food reserves when and where needed, loss of membrane integrity, breakdown of cellular proteins, release and accumulation of cellular toxins produced by membrane damage and oxidative

Table 1: Effect of high temperature on morpho-anatomical and phonological changes in various crops

	Source	Traits affected	References
Morpho-anatomical and phonological changes			
Morphological changes	In different crops	scorching of leaves, sunburns on leaves, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage, and reduced yield	Guilioni et al. (1997) Ismail and Hall (1999), Vollenweider and Gunthardt-Goerg (2005)
	Maize	reduction in dry matter production and yield	Giaveno and Ferrero (2003)
	Maize developing seeds	delayed germination or loss of vigor, ultimately leading to reduced emergence and seedling establishment due to long term effects of heat stress	Weaich et al. (1996)
	Maize, pearl millet and sugarcane	declines in shoot dry mass, relative growth rate and net assimilation rate	Ashraf and Hafeez (2004), Wahid (2007)
	In different crops	reduction in the first internode length resulting in premature death of plants	Hall (1992)
	Sugarcane	smaller internodes, increased tillering, early senescence, and reduced total biomass	Ebrahim et al. (1998)
	Spring wheat	reduced the duration of grain filling with reduction in kernel growth, losses in kernel density and weight upto 7%	Guilioni et al. (2003)
	Wheat	Grain weight, decline in the number of grains per ear at maturity	Ferris et al. (1998)
	Tomato	adversely affected both male and female organs, pollen germination and pollen tube growth, ovule viability, stigmatic and style positions, number of pollen grains retained by the stigma, fertilization and post-fertilization processes, growth of the endosperm, pre-embryo and fertilized embryo	Foolad (2005), Peet and Willits (1998)
	Tomato	Excreted style, poor fruit set and low level of carbohydrates	Kinet and Peet (1997)
	common bean (*Phaseolus vulgaris*)	heat applied prior to anthesis resulted in pollen and anther development abnormalities	Porch and Jahn (2001)
	Linum usitatissimum	affect the reproductive capacity, reduced fruit weight and produce sterile seeds	Cross et al. (2003)
	Arabidopsis thaliana	Decreased leaf biomass may lead to a reduced surface area	Kipp (2006)
	Rice	Exposure to 41°C for 4 h at flowering caused irreversible damage and plants became completely sterile	IRRI (1976)
	Rice	Floret sterility and decreased yield	Nakagawa et al. (2003)
Anatomical changes	In different plants	Reduced cell size, closure of stomata and curtailed water loss, increased stomatal and trichomatous densities, and greater xylem vessels of both root and shoot	Anon et al. (2004)
	Grapes (*Vitis vinifera*)	Damaged the mesophyll cells and increased permeability of plasma membrane	Zhang et al. (2005)
	Zygophyllum qatarense	produced polymorphic leaves, reduce transpirational water loss by showing bimodal stomatal behavior	Sayed (1996)
	Maize	reduced photosynthesis by changing the structural organization of thylakoids	Karim et al. (1997)
	Grape	chloroplasts in the mesophyll cells became round in shape, the stroma lamellae became swollen, and the contents of vacuoles formed clumps, whilst the cristae were disrupted and mitochondria became empty	Zhang et al. (2005)

to continue

Pheno-logical changes	Field pea, *Brassica napus*	During vegetative stage, high day temperature can damage leaf gas exchange properties. During reproduction, a short period of heat stress can cause significant increases in floral buds and opened flowers abortion	Guilioni et al. (1997), Young et al. (2004)
	Tomato	Impairment of pollen and anther development contributing to decreased fruit set	Peet et al. (1998), Sato et al. (2006)
	Cereal crops	damage fertilization and seed production, resulting in reduced yield	Porter (2005)
	Wheat	Modification of flour and bread quality and other physico-chemical properties, including protein content	Perrotta et al. (1998), Wardlaw et al. (2002)

Table 2: Effect of high temperature on physiological responses in various crops

	Source	Traits affected	References
Changes in water status	*Lotus creticus*	reduction in leaf water potential	Anon et al. (2004)
	Sugarcane	leaf water potential and its components were changed, affects the root hydrolic conductivity	Wahid and Close (2007)
	Tomato	perturbed the leaf water relations and root hydraulic conductivity	Morales et al. (2003)
	Snap bean (*Phaseolus vulgaris* L.)	decrease in water potential and leading to perturbation of many physiological processes	Tsukaguchi et al. (2003)
Compa-tible solutes	Maize, sugarcane	high level of glycinebetaine (GB) accumulation	Quan et al. (2004), Wahid and Close (2007)
	Rice (*Oryza sativa*), mustard (*Brassica* spp.), Arabidopsis (*Arabidopsis thaliana*) and tobacco (*Nicotiana tabacum*)	do not produce GB	Sakamoto and Murata (2002), Quan et al. (2004)
	Sugarcane	Proline or GB synthesis may buffer cellular redox potential, accumulation of soluble sugars	Wahid and Close (2007)
	Tomato	Fruit set is failed due to the disruption of sugar metabolism and proline transport during the development of male reproductive organ	Sato et al. (2006)
	In different plants	Increase GABA accumulation through metabolic or mechanical disruptions, thus leading to cytosolic acidification	Kinnersley and Turano (2000)
Photosy-nthetic machinary	Pima cotton	Adversely affected photochemical reactions in thylakoids lamellae and carbon metabolism in the stroma of chloroplast	Wise et al. (2004)
	tropical fruit crops	Chlorophyll fluorescence, the ratio of variable fluorescence to maximum fluorescence (Fv/Fm), and the base fluorescence ($F0$)	Yamada et al. (1996)
	In different plants	chlorophyll fluorescence and root growth potential, gas exchange, electrolyte leakage, visible leaf damage, and leaf water potential	Larcher (1994)
	Tomato and sugarcane	Decresed chlorophyll *a*:*b* ratio and a increased chlorophyll : carotenoids ratio	Camejo et al. (2005), Wahid and Ghazanfar (2006)

to continue

	Maize	degradation of chlorophyll *a* and *b*	Karim et al. (1997 & 1999)
	Tomato	PSII activity is greatly reduced	Bukhov et al. (1999), Camejo et al. (2005)
	Soybean	dissociation of oxygen evolving complex (OEC)	De Ronde et al. (2004)
	Spinach	dissociation of manganese (Mn)-stabilizing 33-kDa protein at PSII reaction center complex	Yamane et al. (1998)
	Barley	abruptly damaged the PSII units, loss of their capacity of oxygen evolution leading to a restricted electron transport	Toth et al. (2005)
	Pima cotton	leaf photosynthesis was limited by photosynthetic electron transport and ribulose-1,5-bisphosphate (RuBP) regeneration capacity, but not rubisco activity	Wise et al. (2004)
	Arabidopsis thaliana, wheat leaves	reduces the amount of photosynthetic pigments, soluble proteins, rubisco binding proteins (RBP) and large- (LS) and small subunits (SS) of rubisco in darkness	Todorov et al. (2003), Kepova et al. (2005)
	Mulbery, soybean leaves	starch or sucrose synthesis is reduced by reducing activities of sucrose phosphate synthase, ADP glucose pyrophosphorylase and invertase	Chaitanya et al. (2001), Vu et al. (2001)
	In any plant species	In vegetative stage, high day temperature can cause damage leaf photosynthesis, reducing CO_2 assimilation rates	Hall (1992)
	Maize, tomato	increase CO_2 transfer conductance between intercellular spaces and carboxylation sites, stomatal conductance (gs) and net photosynthesis (Pn) are inhibited	Crafts-Brander and Salvucci (2002), Morales et al. (2003)
	Soybean	dissociation of the oxygen evolving complex (OEC), resulting in an imbalance during the electron flow from OEC toward the acceptor side of photosystem II	Ronde et al. (2004)
Assimilate partitioning	Wheat	reduced grain filling by examining source (flag leaf blade), sink (ear), and transport pathway (peduncle)	Wardlaw (1974)
	Wheat	effects on translocation, source and sink activities	Yang et al. (2002)
Cell membrane thermo stability	Soybean; potato and tomato; wheat; cotton; sorghum, cowpea and barley respectively	alters the tertiary and quaternary structures of membrane proteins leads to enhance the permeability of membranes, as evident from increased loss of electrolytes and decreased cell membrane thermo stability (CMT)	Martineau et al. (1979), Chen et al. (1982), Blum et al. (2001), Ashraf et al. (1994), Marcum (1998), Ismail and Hall (1999), Wahid and Shabbir (2005)
	Maize mature leaves	injuries to plasmalemma	Karim et al. (1997 & 1999)
	Arabidopsis thaliana	total lipid content in membranes decreased to about one-half and the ratio of unsaturated to saturated fatty acids decreased to one-third of the levels at normal temperatures	Somerville and Browse (1991)
	Sorghum, soybean, wheat	Cell membrane thermo stability (CMT) and yield	Sullivan and Ross (1979), Martineau et al. *(*1979), Shanahan et al. (1990)
Hormonal changes	Cereals	Hormonal homeostasis, stability, content, biosynthesis and compartmentalization	Maestri et al. (2002)

to continue

	Bentgrass (*Agrostis palustris*)	ABA accumulation upon recovery	Larkindale and Huang (2005)
	Plants	ABA-responsive promoters revealed several potential *cis*- and *trans*-acting regulatory elements	Swamy and Smith (1999)
	Arabidopsis thaliana	ABA mediated up- or down-regulation of numerous genes	Xiong et al. (2002)
	Rice	Induction of several HSPs (e.g., HSP70) by ABA	Pareek et al. (1998)
	Sunflower embryo	Heat shock transcription factor 3 acts synergistically with chimeric genes with a small HSP promoter induced by ABA	Rojas et al. (1999)
	Rosemary (*Rosmarinus officinalis*)	Increase in endogenous concentration of 1-amino-cyclopropane-1-carboxylic acid (ACC) (a precursor of ethylene biosynthesis)	Munne-Bosch et al. (2002
	Soybean, wheat	Ethylene production in hypocotyls increased in soybean, ACC accumulated in both species at 40 °C	Tan et al. (1988)
	Creeping bentgrass	Ethylene production reduced	Larkindale and Huang (2005)
	kiwifruit	Inhibits ripening by inhibiting ethylene production	Antunes and Sfakiotakis (2000)
	Pepper (*Piper nigrum*)	Increase in the level of ACC	Huberman et al. (1997)
	Imbibed sunflower seed	Loss of seed’s ability to convert ACC to ethylene at 45°C	Corbineau et al. (1989)
	Pepper reproductive organ	Induced abscission of reproductive organs relates to an increased ACC level	Huberman et al. (1997)
	Apple	Sun-exposed apple fruits accumulate 90% more ethylene	Klein et al. (2001)
	Young grape plant	SA stabilizes the trimers of heat shock transcription factors, Ca^{2+} homeostasis and antioxidant systems	Wang and Li (2006b)
	Cucumber (*Cucumus sativus*)	Sulphosalicylic acid (SSA) remove H_2O_2 and increase heat tolerance	Shi et al. (2006)
	Holm oak, grape	Methyl salicylate (MeSA) involved thermotolerance to holm oak (*Quercus ilex*) by enhanced xanthophylls de-epoxidation and content of ascorbate, antioxidants and α-tocopherol in leaves	Llusia et al. (2005), Wang and Li (2006a)
	Tomato and oilseed rape (*Brassica napus*)	Brassinosteroids increased thermotolerance	Dhaubhadel et al. (1999)
	Dwarf wheat	High temperature- induced decrease in cytokinin content responsible for reduced kernel filling and dry weight	Banowetz et al. (1999)
Secondary metabolites	Watermelon, *Citrulus vulgaris*	biosynthesis of phenolics (increased activity of PAL) and suppresses their oxidation	Rivero et al. (2001)
	In many plants	the xanthophylls including violaxanthin, antheraxanthin and zeaxanthin partition between the light-harvesting complexes and the lipid phase of the thylakoid membranes. The resulting interaction of the xanthophyll molecules and the membrane lipids brings about a decreased fluidity (thermostability) of membrane and a lowered susceptibility to lipid peroxidation under high temperatures	Havaux (1998)
	Tomato, watermelon	accumulation of soluble phenolics under heat stress was accompanied with increased phenyl ammonia lyase (PAL) and decreased peroxidase and polyphenol lyase activities	Rivero et al. (2001)
	Aster flower	Accumulation of anthocyanins	Sachray et al. (2002)

to continue

	Red apple, chrysanthemums and aster	Decreases synthesis of anthocyanins in reproductive parts	Tomana and Yamada (1988), Shibata et al. (1988), Sachray et al. (2002)
	Rose, sugarcane	Accumulation of anthocyanins in vegetative parts	Wahid and Ghazanfar (2006)
	In different plants	Anthocyanins serve to decrease leaf osmotic potential	Chalker-Scott (2002)
	In different plants	Isoprenoids emission from leaves protect photosynthesis apparati	Loreto et al. (1998)
	Phragmites australis leaves	Endogenous production of isoprene protects the biological membranes from damaging effects by directly reacting with oxygen singlets ($^1O_2$)	Velikova et al. (2005)

Table 3: Effects of high temperature on molecular responses, stress proteins, acquired thermotolerance and temperature sensing and signalling

	Source	Traits affected	References
Oxidative stress and antioxidants	Creeping bent grass	generation and reactions of activated oxygen species (AOS) including singlet oxygen ($^1O_2$), superoxide radical (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^-) are symptoms of cellular injury	Liu and Huang (2000)
	Turfgrass	AOS cause the autocatalytic peroxidation of membrane lipids and pigments thus leading to the loss of membrane semi-permeability	Xu et al. (2006)
	Tomato	expression and activation of APX is related to the appearance of physiological injuries	Mazorra et al. (2002)
	Turfgrass	heat-acclimated lower production of ROS as a result of enhanced synthesis of ascorbate and glutathione	Xu et al. (2006)
Stress proteins			
Heat shock proteins	Maize, wheat and rye	Five mitochondrial LMW-HSPs (28, 23, 22, 20 and 19 kDa) were expressed in maize, only one (20 kDa) was expressed in wheat and rye	Korotaeva et al. (2001)
	Tomato	HSPs aggregate into a granular structure in the cytoplasm, protecting the protein biosynthesis machinery	Miroshnichenko et al. (2005)
	Potato, maize, tomato, soybean and barley	HSP68, localized in mitochondria and increased expression under heat stress	Neumann et al. (1993)
	Maize	HSP101 more abundantly in developing tassel, ear, silks, endosperm and embryo and less abundantly in vegetative and floral meristematic regions, mature pollen, roots and leaves	Young et al. (2001)
	Maize	Increase the level of 45-kDa HSP	Ristic and Cass (1992)
	Maize	elongating segments of primary roots exhibited a strong ability to synthesize nucleus-localized HSPs	Nieto-Sotelo et al. (2002)
	Maize	synthesis of a typical set of HSPs was induced in male tissues of maize flowers undergoing pollen formation, the mature pollen showed no synthesis of HSPs and thus were sensitive to heat stress and responsible for the failure of fertilization at high temperatures	Dupuis and Dumas (1990)

to continue

	Germinating maize pollen	induction of 64 and 72 kDa peptides of HSPs	Frova et al. (1989)
	Grape	Accumulation of HSP70 influence protein translation and translocation, proteolysis, protein folding or chaperoning, suppressing aggregation, and reactivating denatured proteins	Zhang et al. (2005)
	Tomato	LMW HSP21 protect PSII from oxidative damage	Neta-Sharir et al. (2005)
	Higher plants	HSP70 participates in ATP-dependent protein unfolding or assembly/disassembly reactions and it prevents protein denaturation	Iba (2002)
	Maize	Accumulation of HSP22	Lund et al. (1998)
	Chenopodium album	LMW-HSPs in chloroplast membranes protects the PSII from adverse effects of heat stress and act in photosynthetic electron transport	Barua et al. (2003)
Other heat induced proteins	*Prosopis chilensis* and soybean	ubiquitin and conjugated-ubiquitin synthesis during the first 30 min of exposure	Ortiz and Cardemil (2001)
	Higher plants	Mn-peroxidase, plays a vital role in minimizing oxidative damages	Iba (2002)
	Chenopodium murale	Cu/Zn-SOD from stromal fraction was more heat tolerant than Cu/Zn-SOD from thylakoid, and this was responsible for chloroplastic stability	Khanna-Chopra and Sabarinath (2004)
	Tobacco	a number of osmotin like proteins (called Pir proteins), were overexpressed under heat stress	Yun et al. (1997)
	In many plants	Late embryogenesis abundant (LEA)proteins can prevent aggregation and protect the citrate synthase from desiccating conditions	Goyal et al. (2005)
	Hexaploid wheat, Geranium leaves	enhanced expressions of 25 LEA proteins during grain filling stage; dehydrin proteins (25–60 kDa)	Arora et al. (1998)
	Sugarcane	three low-molecular-weight dehydrin proteins are expressed	Wahid and Close (2007)
Acquired thermotolerance			
	Arabidopsis mutants	heat shock proteins (HSP32 and HSP101), ABA, ROS and SA pathways are involved in the development and maintenance of acquired thermotolerance	Larkindale and Huang (2005), Charng et al. (2006)
	In higher plants	The heat shock response (HSR), defined as a transient reprogramming of gene expression, is a conserved biological reaction of cells and organisms to elevated temperatures	Sch¨offl et al. (1999)
Temperature sensing and signaling			
	In higher plants	Signaling of the stress via the redox system. Chemical signals such as ROS, Ca^{2+} and plant hormones activate genomic re-programing via signal cascades	Joyce et al. (2003), Suzuki and Mittler (2006)

to continue

		Changing membrane fluidity plays a central role in sensing and influencing gene expression; sensors are located in microdomains of membranes, which are capable of detecting physical phase transition, eventually leading to conformational changes and/or phosphorylation /dephosphorylation cycles due to changes in temperature	Plieth (1999)
		Rigidification of thylakoid membranes appears to invoke altered expression profiles of heat shock genes	Horvath et al. (1998)
	Creeping bentgrass	Cytosolic Ca^{2+} sharply rises by transducing high temperature-induced signals to MAPK	Larkindale and Knight (2002)
		MAPK cascades are important parts of signal transduction pathways in plants	Kaur and Gupta (2005)
		Heat-shock activated MAPK (HAMK) has been changeed in membrane fluidity coupled with cytoskeletal remodelling; Ca^{2+} influx and the action of Ca-dependent protein kinases (CDPK) have been correlated with the expression of HSPs	Sangwan and Dhindsa (2002)
	Maize	heat stress induces uptake of Ca^{2+} and induction of some calmodulin (CaM) related genes	Gong et al. (1997)
	In higher plants	Increasing cytosolic Ca^{2+} content under heat stress may alleviate heat injury, such as increased activity of antioxidants, turgor maintenance in the guard cells enable plant cells to better survive	Gong et al. (1997), Webb et al. (1996)
	Pepper	Excessive Ca^{2+} released into the cytosol and sustained high cytosolic Ca^{2+} concentration might be cytotoxic	Wang and Li (1999)
	Agrostis stolonifera	signaling molecules like SA, ABA, $CaCl_2$, H_2O_2, and ACC may induce tolerance of plants to heat stress by reducing oxidative damage	Larkindale and Huang (2004)
	Holm oak	Methyl-SA has a major signaling role in the gene activation under heat stress	Llusia et al. (2005)

Table 4: High temperature tolerant transgenics

Gene	Protein	Source	Cellular function	Trans host	Promoter	Comments	Reference
Using HSFs and Hsps							
Athsf1	HSF	*A. thaliana*	TF	*A. thaliana*	CaM-V35S	Transformants exhibited. thermotolerance and also constitutive expression of the *hsp* genes at normal temperature.	Lee et al. (1995)
Athsf3	HSF	*A. thaliana*	TF	*A. thaliana*	CaM-V35S	*Arabidopsis* plants showed an increase in basal thermotolerance, indicating the importance of HSFs and HSF-regulated genes as determinants of thermoprotective processes.	Prandl et al. (1998)

to continue

AtHsfA2	HSF	*A. thaliana*	TF	*A. thaliana*	CaM-V35S	The mutants displayed reduced basal and acquired thermotolerance as well as oxidative stress tolerance while the over expression lines displayed increased tolerance.	Li et al., (2005)
OsHSFA2e	HSF	*O. sativa*	TF	*A.thaliana*	Maize Ubi 1	Arabidopsis plant showed enhanced thermotolerance	Yokotani et al. (2007)
HsfA1	HSF	*S. lycopersi-con*	TF	*S. lycopersicon*	CaMV35S	HsfA1 over-expression in plants provided distinct advantage to growth and fruit ripening processes under high temperature stress conditions; in case of HsfA1 cosupression, plants and fruits were sensitive to elevated temperatures	Mishra et al. (2002)
HSF3	HSF	*A. thaliana*	TF	*A.thaliana*	CaMV35S	HSF3 over-expressing plants showed a lower threshold temperature for the expression of HSPs than wild type plants along with the presence of a novel heat stress induced thermostable isoform of ascorbate peroxidase which was absent in the wild type	Panchuk et al. (2002)
TLHS1	TLHS1	*N. tabacum*	Chap-erone	*N. tabacum*	CaMV35S	Over-expressing plants showed significant increase in thermotolerance as was evident by the rate of cotyledon opening after heat stress treatments. Antisence plants showed severe defect in withstanding stress	Park and Hong (2002)
Hsf17.7	HSP17.7	*Dau-cus carota*	Chap-erone	*Daucus carota*	CaMV35S	Transformants expressed *hsp17.7* gene in the absence of heat shock and showed increased thermotolerance.	Malik et al. (1999)
sHSP	Mt-sHSP	*S.lycopersicon*	Chap-erone	*N.tabacum*	CaMV35S	Plants which over-express the MT-sHSP gene exhibited thermotolerance, while the antisense plants in which the expression of the gene was suppressed exhibited susceptibility.	Sanmiya et al. (2004)
hsp21	HSP21	*S.lycopersicon*	Chap-erone	*S.lycopersicon*	CaMV35S	Protects PSII from temperature-dependent oxidative stress; also plays role in accumulation of carotenoids during fruit ripening	Neta-Sharir et al. (2005)

to continue

hsp101	HSP-100	*A. thaliana*	Chap-erone	*A. thaliana*	CaMV35S	Transformants constitutively expressing hsp101 tolerated sudden shifts to extreme temperature better than the controls	Quietsch et al. (2000)
hsp101	HSP-100	*A. thaliana*	Chap-erone	*O. sativa*	Maize Ubi 1	Transformants expressing hsp 101 showed enhanced tolerance to high temperature	Katiysr-Agarwal et al. (2003)
Using proteins involved in ROS scavenging system							
Cu/Zn SOD	Cu/Zn superoxide dismutase	*Manihot esculenta*	ROS scavenging en-zyme	*Sola-num tuberosum*	SWPA2 (oxidative stress inducible)	Transgenic plants showed enhanced tolerance to 250 μM methyl viologen, and visible damage in these transgenic plants was one-forth that of non-transgenic plants that were almost destroyed	Tang et al. (2006)
APX	Ascorbate peroxidase	*Pisum sativum*	-	-	-	-	-
HvAPX1	Ascorbate peroxidase	*Hordeum vulgare*	H_2O_2 detoxification	*A. thaliana*	CaMV35S	Ascorbate peroxidase is involved in detoxification of photo-produced H_2O_2. Transgenic plants were significantly more tolerant to heat stress	Shi et al. (2001)
Using protein involved in osmolytes synthesis							
badh	Betaine aldehyde dehydrogenase	*Spinacia oleracea*	Glycine-betaine synthesis	*N. tabacum*	CaMV35S	Transgenic plant accumulated glycinebetaine mainly in chloroplasts, which resulted in enhanced tolerance to high temperature stress during growth of young seedlings	Yang et al. (2005)
cod A	Choline oxi-dase	*A.globiformis*	Glycine-betaine synthesis	*A. thaliana*	CaMV35S	Transformants showed tolerance to high temperature during imbibition and germination of the seeds	Alia et al. (1998)

to continue

fad 7	ω-3-fatty acid desaturase	*A. thaliana*	Causes reduction of trienoic fatty acids and hexadecatri-enoic acid	*N. tabacum*	CaMV35S	Transformants showing silencing of the gene were better able to acclimate to higher temperature	- et al. (2000)
fad 7	ω-3-fatty acid desaturase	*A. thaliana*	Causes reduction of trienoic fatty acids and hexadecatr-ienoic acid	*O. sativa*	Maize Ubi 1	Transformants showing silencing of the gene showed better chlorophyll content and photochemical efficiency	Sohn and Bach (2007)
fad 8	Desaturase	*Brassica napus*	- acting on paired donors, with incorporation or reduction of molecular oxygen	*N. tabacum*	CaMV35S	Over-expression of FAD8 imposes much greater heat sensitivity than does FAD3 over-expression	Zhang et al. (2005)
Others							
mbf1c	Multiprotein bridging factor 1c	*A.thaliana*	Transc-ription regulation	*A.thaliana*	CaMV35S	Enhances the tolerance of transgenic plants to bacterial infection, heat and osmotic stress. The enhanced tolerance of transgenic plants to osmotic and heat stress was maintained even when these two stresses were combined	Suzuki et al. (2005)
fld	Flavodoxin	*Anabaena*	Electron carrier	*N. tabacum*	CaMV35S	Tobacco plants expressing Fld in chloroplasts displayed increased tolerance to multiple sources of stress, including redox-cycling herbicides, extreme temperatures, high irradiation, water deficit and UV radiation	Tognetti et al. (2006)
SBPase	Sedoheptulose-1,7-bisphosphatase gene	*O. sativa*	Calvin cycle	*O. sativa*	Maize Ubi1	Transgenic plants were more tolerant to high temperature stress during seed development	Feng et al. (2007)
rolB	B-glucosidase	*Agrobacterium rhizogenes*	Root formation	*S. lycopersicon*	TPRP-F1(early fruit specific promoter)	Transgenic line expressing rolB specifically during early stages of fruit development performed significantly better than the parental line at both high and low temperatures	Shabtai et al. (2007)

reactions and inhibition growth. However, these effects of heat stress to plant system, studied by various workers to know more about the facts actually happening by integrating the knowledge of physiology, biotechnology and molecular biology; those are summarized in the present review in tabular form within the following framing

2. Conclusion

In the advent of global warming caused by increase in atmospheric CO_2, heat stress poses a serious threat to life on earth nevertheless to say the crop growth and productivity. Though many heat shock proteins are identified during the course of investigation still a lot of scope is there to know more about it by studying those plants, which grow in high temperature zone. Different biotechnological and molecular interventions towards development high temperature tolerant genotypes can be possible by understanding of the diverse functions of Hsf, which along with other transcription factor, form a set of regulatory network, essential for plants survival and development in a particular thermal zone.

3. References

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