Heat stress in cultivated plants: nature, impact, mechanisms, and mitigation strategies—a review

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ABSTRACT

The progressive increase in the earth's temperature due to anthropogenic activities is a major concern for humanity. The ensuing heat stress (HS) severely impacts plant growth, endangering ecosystem quality and world food security. Plant growth, physiological processes and final amount of edible products are affected by HS to an extent that reflects the physical damages, physiological

1

commotions and biochemical alterations incurred at various growth stages. Therefore, a better understanding of plant behaviour in response to HS has pragmatic implications for devising counter-measures, alleviation strategies, and for acknowledging the differences between HS and the companion drought stress. Conventional breeding, biotechnological and molecular approaches are used to develop HS tolerant genotypes in plant species bred for food/feed uses. Recent achievements in the omics techniques result in a better knowledge of the molecular mechanisms involved in HS. However, shrewd management of crop practices is still helpful to improve plant resilience to HS. Suitable sowing time, seed priming, bacterial seed treatment, nutrient and water management, exogenous application of osmo-protectants, and conservation of soil moisture are important tools to improve plant behaviour under the critical HS scenarios determined by climate change and global warming.

Keywords: Crop production, Heat stress, Heat shock proteins, Heat stress management, Oxidative damage, Reproduction, Plant response

Introduction

The harshly debated fossil fuel usage due to booming population and anthropogenic activities, is the major reason for the global warming associated with changing climate patterns. Climate change and global warming have devastating impacts on food security (Lesk et al. 2016). Over the last 250 years, carbon dioxide and methane concentrations in the atmosphere have been increasing by 30% and 150%, respectively (Friedlingstein et al. 2010). The increase in greenhouse gases concentration is the major reason for global warming. In this scenario, heat stress (HS) has become a major factor limiting crop production and food security around the globe. The recent increase in temperature severely endangers regional crop productions (Lobell et al. 2011a; Abdelrahman et al. 2017). Globally, annual temperature is expected to rise by 1.8-4.0 °C at the end of the 21st century (Bita and Gerats 2013). This increase raises the concern among scientists and governments, as temperature directly and indirectly impacts on life forms present on earth. Despite these happenstances, world food supply has to be augmented by more than 70% to meet the needs of ever booming population: up to 9 billion humans by the year 2050 (Stratonovitch and Semenov 2015).

Heat stress severely limits the productivity of crop plants. For example, it is assumed that HS limits wheat (*Triticum aestivum* L.) global productivity by more than 6% for each degree (°C) increase in temperature (Asseng et al. 2015). However, despite HS negative effects on overall crop production, increase in temperature has some beneficial impacts on productivity in colder regions (Challinor et al. 2014).

Plants, being sessile organisms cannot move to favourable conditions, thus their activities are significantly affected by HS (Lobell and Field 2007; Hatfield and Prueger 2015). Heat stress significantly affects plant activities including seed germination, growth, development,

3

photosynthesis, reproduction, resulting in serious impacts on plant growth and ultimate yield of useful products (Fig. 1) (Hasanuzzaman et al. 2012). Therefore, for surviving under stressed conditions, plants perform various morphological, physiological and molecular responses (Fig. 2) (Janská et al. 2010). Specific field management options can be practiced to get good production under stressed conditions.

Fig 1 has to be placed here

Moreover, development of heat tolerant genotypes requires a dire need of knowledge and research work at physiological, bio-chemical and molecular level. In the present scenario, more investigations are needed for breeding HS tolerant genotypes, and understanding general mechanisms supporting HS tolerance in plants. In the present circumstances, developing heat tolerant genotypes is a major challenge for the experts (Zhang et al. 2006). In the upcoming time, agriculture has to deal with crops growing under sub-optimal conditions in face of enhanced food demand, which creates a gap between the current yield accomplishment and yield potential (Koevoets et al. 2016). In this review, we discuss the effects of HS, along with plant response to HS, and potential management options to enhance the resilience of cultivated plants under the current scenario of global warming.

Yield losses due to heat stress: region wise retrospective and future projections

The unprecedented increase in air temperature in the last few years reveals a range of incongruities linked with HS. The negative impacts of high temperature (HT) on different crops have been reported globally (Table 1). In the case of rice (*Oryza sativa* L.), China is a major growing country, and rapid increase in temperature during the last few years caused a significant reduction in rice production (Tian et al. 2009). High temperature at late growth stages reduces rice yield owing to

4

lower seed production resulting from pollen sterility (Tian et al. 2009). Similarly, analysis of data from 1980-2000 indicates that 1% increase in temperature is responsible for the reduction in wheat yield by more than 10% (You et al. 2009) in China. Likewise, Easterling et al. (2007) projected that India will lose 0.45 ton/ha and China will face a reduction of 5-7% in rainfed wheat production, owing to a 0.5% rise in average temperature by the end of 2050. High temperature (38-39 °C) in the Philippines during the months of April and May poses a serious threat to rice production (Manigbas and Sebastian 2007). More to this, the Indo Gangetic Plains (IGP) produce 15% of world wheat and will face drought and HT conditions by the end of 2050 (Ortiz et al. 2008). Climatic models also predict that Central and East Asia, North American and the Indian subcontinent will be areas most prone to HS among those growing the major crops rice, wheat and maize (Teixeira et al. 2013).

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The European continent faced a very hot summer in 2003 leading to considerable reduction in yield (Ciais et al. 2005). In the near future, devastating effects of HS on crop yields are envisaged with alarming frequency for East European countries as Hungary, Serbia, Bulgaria and Romania (Olesen et al. 2011). In Western Europe as France; significant reductions in maize (*Zea mays* L:) yield were observed, and are likely to be incurred again, at temperatures above 32 °C (Hawkins et al. 2013). The maturation period for wheat is shrinking in Europe, seriously affecting crop yields (Semenov et al. 2013). It is further feared that Europe as a whole will experience major crop losses engendered by HS more than drought stress (Semenov and Shewry 2011). In Africa, various traits combined lead to predict a more than 2% reduction in maize yield as consequence of a 1% rise in temperature (Lobell et al. 2011a). The pattern of temperature changes during 1976-2006 indicates a reduction of 12% and 17% in maize and soybean (*Glycine max* (L.) Merr.) production in the

USA (Kucharik and Serbin 2008). Similarly, the southern and south-western region of the USA will face a loss of more than 5 billon US dollars owing to combined HS and drought stress (NCDC 2011). It is therefore demonstrated that the present and future increases in temperature will have negative impacts on crop production. Therefore, there is a dire need to change the policies globally and work collectively to cope with this problem.

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Heat stress effects on growth and development of plants

Seed germination is the first stage of plant life that may be severely affected by HS. The HS has negative impacts on seed germination over a broad range of temperatures; however, the extent of the damage largely depends on plant species (Johkan et al. 2011). HS leads to poor seed germination resulting in reduced root length, poor stand establishment, lower plant population and, therefore, significant reduction in final yield (Kumar et al. 2011; Toh 2008). HS reduces seed germination by disturbing the activity of various enzymes that are responsible for the breakdown of starch, as well as inducing abscisic acid (ABA) synthesis (Essemine et al. 2010). HS also impaired protein synthesis in seed embryo and led to a substantial reduction in seed germination of maize above 37 °C (Riley et al. 1981). The growth of coleoptile was completely stopped at 45 °C in maize seedlings (Akman 2009). At this temperature, germination rate was greatly reduced and cell death occurred in tomato (*Solanum lycopersicum* L.), leading to significant decline in stand establishment (Cheng et al. 2009). Additionally, HS reduced plant height, tillering, and dry biomass production in wheat (Mitra et al. 2008).

Heat stress reduced cell size and water status, leading to growth reduction in maize and pearl millet (*Pennisetum glaucum* (L.) R. Br.) (Ashraf and Hafeez 2004). Moreover, reduction in crop growth

6

rate and dry matter production occurred owing to HS in various plants (Wahid 2007), and specifically sugarcane (*Saccharum officinarum* L.) (Srivastava et al. 2012). HS also causes many morphological symptoms in plants: leaf scorching, sun burning of stems, branches, leaves and twigs, discoloration of fruits, leaf senescence and abscission (Rodríguez et al. 2005). Leaf rolling, damage of leaf tips, leaf drying and necrosis can also be observed due to HS (Omae et al. 2012). In few plant species, HS (30 °C) significantly elongated the stem and bended plant leaves (hyponasty), and therefore, resulted in significant reduction in biomass production (Patel and Franklin 2009). The decrease in tillers with surge in shoot elongation is also a common symptom of HS (Kumar et al. 2011). For instance, in wheat crop tillers decreased per unit area owing to increase in shoot elongation under HS (30/25 °C at day/night time) (Djanaguiraman et al. 2010). HS also affected plant phenology, shortening plant cycle. For instance, increase in temperature (1-2 °C) above the optimum level decreased the grain filling period in cereals, resulting in final production significantly reduction (Zhang et al. 2006). At extreme HS, programmed cell death occurs in specific cells and tissues, owing to protein denaturation. Under moderate HS for a longer time, a gradual death is observed. Therefore, both severe and moderate HS lead to leaf shedding, flower and fruit abortion and death of complete plant (Hasanuzzaman et al. 2010).

Heat stress in maize reduced photosynthesis while increasing respiration, causing pollen sterility and lower kernel development (Crafts-Brander and Salvucci 2002). In soybean, HS at later growth stages (grain filling stage) reduced the subsequent seed germination and seedling vigor (Egli et al. 2005). The increase in temperature above 30 °C obstructed micro-sporogenesis in common beans (*Phaseolus vulgaris* L.) (Porch 2006) groundnut (*Arachis hypogaea* L.), sorghum (*Sorghum bicolor* (L.) Moench) (Prasad et al. 2008b), and cotton (*Gossypium* spp.) (Singh et al. 2007). HS at later stages increased pollen sterility and decreased the number of kernels, kernel size and weight

7

in wheat (Farooq et al. 2011). Additionally, HS also causes various types of irregularities, among which degradation of tapetum during the microsporic-meiosis (Zinn et al. 2010), and reduction in starch accumulation at grain filling stage (Reynolds et al. 2007). The reduction in seed production due to HS is also associated with hindrance in the fertility of micro and mega gametophyte (Young et al. 2004; Hayat et al. 2009). In conclusion, HS dramatically reduces plant growth and cycle length. Therefore, proper measures should be adopted to improve crop production under HS.

Heat stress effects on water relations

Heat stress affects plant osmotic adjustments by enhancing evapotranspiration (Gates 1968), while influencing the production of solutes as glucose that plays an imperative role in osmotic adjustment (Acevedo et al. 1999). The rate of photosynthesis is decreased (Paulsen 1994), as those of respiration and photo-respiration (Lawlor 1979), while leaf senescence is significantly hastened (Kramer 1980). All these factors alter solute production for osmotic adjustment. Heat stress is directly detrimental for all crops, by altering plant water relationships and affecting various physiological processes (Paulsen 1994). HT reduces photosynthesis and plant growth, and disturbs plant water relationships depending upon crop species and genotype (McDonald and Paulsen 1997).

Heat stress disturbs cell metabolism owing to hampered water balance resulting from reduction in water uptake by roots and additional water loss from leaves (Machado and Paulsen 2001). HS also hampers leaf water potential (Wahid and Close 2007), and increases the fluidity of membrane lipids (Xu et al. 2006) and the production of reactive oxygen species (ROS) (Wahid et al. 2007). All these alterations lead to reduction of plant growth (Young et al. 2004; Porter 2005).

Drought and HS are two of the major constraints for crop production. However, drought stress escorts HS particularly in the summer season (Jedmowski et al. 2015). Drought and HS lead to dehydration, reduced relative water content (RWC), augmented leaf senescence owing to lower chlorophyll content and photo-synthetic activity, and reduction in membrane stability (Pessarakli 2007; Rivero et al. 2007; Veerasamy et al. 2007). HT results in quick loss of soil water, which interacts with drought and HS in reducing tissue moisture and leaf water potential (Machado and Paulsen 2001; Wahid and Shabbir 2005). HT also exerts a negative influence on stomatal density, pore spaces and conductance of stomata, and all these changes have direct effect on water loss from plants (Sharma et al. 2014; Zhou et al. 2017). HT also reduces the RWC and total water absorption rate, which leads to serious reduction in final yield (Ashraf and Hafeez 2004).

Heat stress effects on nutrient uptake

High temperature stress reduces water and nutrient uptake, resulting in significant reduction of plant growth (Huang et al. 2012). Moreover, HT alters plant source-sink relationships, reduces the amount of hormones produced in roots, and affects plant nutrient concentration (Huang et al. 2008; Rennenberg et al. 2006).

Less research has been devoted to determine the effects of HS on roots than shoots, and past research has mostly focused on the effect of HS on root growth and carbon metabolism, especially respiration (Huang et al. 2008). Only a few authors studied how HS affects plant nutrient relationships (Bassirirad 2000; Huang et al. 2008; Rennenberg et al. 2006) and most of these investigations were performed to study the effects of HS on nutrient concentrations. Additionally, most of the past studies were conducted on the roots in response to chronic HS. However, the

response to abrupt HS that may differ from chronic HS in the uptake of nutrient by plant roots (Wahid et al. 2007), is still poorly understood.

Heat stress often decreases the concentration of important nutrients in plants; sometimes it also reduces the total nutrient content in plants. However, the extent of these effects depends on specific nutrients and plant species. HS disrupts the enzymes involved in nutrient metabolism (e.g., nitrate and ammonium assimilation) and therefore, decreases nutrient uptake (Klimenko et al. 2006; Hungria et al. 2014). Additionally, HS decreases nutrient acquisition possibly due to reductions in root biomass, root hair surface, and nutrient uptake per unit root (Bravo and Urib 1981). HS reduces nutrient uptake per unit root area owing to depletion of labile carbon (non-structural carbohydrates). Moreover, HS also restricts the transport of carbohydrates from the shoots to roots and directly affects plant roots (Huang et al. 2008), decreasing production and functions of nutrient uptake proteins. In turn, the reduced activity of nutrient uptake proteins decreases nutrient uptake. However, the effect of HS on nutrient uptake proteins is still unclear and needs to be further explored in future (Huang et al. 2008).

Heat stress effects on photosynthesis

Photosynthesis is the most important process in plant physiology, and is also highly sensitive to HS (Crafts-Brandner et al. 2002). HT strongly influences the photosynthetic efficiency of C_3 and C_4 plants (Yang et al. 2006). Carbon metabolism in stroma and reactions taking place in the thylakoids are the primary activities affected by heat injury (Wang et al. 2009). HT results in major alterations in the chloroplast: disorganization of thylakoid, grana swelling and loss (Table 2) (Rodríguez et al. 2005). The activity of photo-system II significantly declines or stops under HS, in turn reducing the photosynthetic pigments (Marchand et al. 2005).

High temperature also decreases leaf water content, conductance of stomata and inter-cellular CO_2 concentration (Greer et al. 2012). Moreover, stomata close under HS, which impairs photosynthesis and significantly affects the concentration of intercellular CO_2 (Ashraf et al. 2004). HS also leads to loss of chlorophyll pigments owing to lipid peroxidation in membranes and chloroplasts (40/30 °C, day/night) (Table 2). HT substantially reduces the Fv/Fm ratio in fluorescence, which leads to significant reduction in photosynthesis (Mohammed et al. 2010). HT (38 °C) in soybean reduced the photosynthetic pigments, Fv/Fm ratio, and stomatal conductance (gs), leading to a reduction in the final production (Tan et al. 2011). Different authors also reported that HS reduced the rate of photosynthesis in rice (Hurkman et al. 2009) and grape vine (*Vitis vinifera* L.), owing to stomatal closure (Kepova et al. 2005). HS-induced reduction in photosynthesis is related to the reduction in soluble proteins, Rubisco binding protein (RBP), small and large sub-units of RBP (Table 2) in light and darkness (Sumesh et al. 2008). HS also reduces the activity of various enzymes (phosphate synthase, ADP-glucose pyrophosphorylase, and invertase), and therefore leads to reduction in the synthesis of starch and sucrose (Djanaguiraman et al. 2009).

Table 2 has to be placed here

High temperature also affects plant water relations; i.e., it reduces the water potential, leaf area, and these factors lead to reduction in photosynthesis (Young et al. 2004). Additionally, under long HS the carbohydrate reservoirs are depleted, which is also responsible for reduction in photosynthesis (Djanaguiraman et al. 2009). Under HS, chlorophyll *a* and *b* are degraded at a faster pace (Table 3) (Karim et al. 1999), the degradation being accompanied by the production of ROS (Guo et al. 2006). HS alters the distribution of energy and the activities of various enzymes including Rubisco, thus changing the regeneration rate of RuBP by disrupting the electron

transport chain, and in-activating the oxygen evolving enzymes of PS-II (Salvucci and Crafts-Brandner 2004).

High temperature decreases photosynthesis, while increasing the transfer conductance of CO_2 towards the carboxylation sites. Moreover, gs and net photosynthesis (Pn) are strongly hampered by HS, because of decreasing activity of Rubisco (Morales et al. 2003). The high temperature also increases the catalytic activity of Rubisco.

Nevertheless, lower affinity of Rubisco for CO_2 and its dual nature as oxygenase counter the potential increase in Pn. In maize, for instance, Pn was inhibited above 38 °C, and the inhibition was stronger upon abrupt than gradual temperature increase (Morales et al. 2003). Generally, the photosynthesis rate significantly decreases while the rate of photo-respiration remarkably increases under HT, which is one of the most noticeable consequences of HS. Moreover, HT enzymatic inactivation and denaturation significantly increase, while the rate of bio-chemical reactions decreases, which also leads to reduction in photosynthesis (Nakamoto and Hiyama 1999). Nonetheless, effect and magnitude of these changes vary significantly with species and genotype (McDonald and Paulsen 1997). The rising CO_2 concentration will further increase the ambient temperature that will, in turn, significantly influence crop production and distribution of vegetable species in coming time.

Table 3 has to be placed here

Heat stress effects on assimilate partitioning

Heat stress significantly reduces the source-sink activities, ultimately leading to serious reduction in plant growth and final production (Taiz and Zeiger 2006). Nonetheless, considerable disparities have been reported in assimilate partitioning under HS conditions (Yang et al. 2002). HS affects

12

plant source and sink relations by reducing the C assimilation and partitioning, and re-distribution of C and N in plants (Calderini et al. 2006). These variations negatively affect protein and starch metabolism in leaves, which are the premises for serious reductions in yield and quality (Yang et al. 2011). The single kernel weight, and total grain yield, depend on sustained Pn during grain filling, and re-translocation of assimilates from vegetative organs, as water soluble carbohydrates (WSC) stored in plant stem before grain filling (Fischer 2011). Therefore, genotypic variations for grain weight are associated with differences in photosynthesis and re-translocation of stored carbohydrates under HS conditions (Dreccer et al. 2009).

Under normal conditions, stem reservoirs contribute 30-40% to grain weight (Dreccer et al. 2009). However, under HS the contribution of stem stored carbohydrates increases up to 70% (Rebetzke et al. 2008). Likewise, C transport to plant apex was significantly reduced under HS in tomato (Dinar and Rudich 1985; Fahad et al. 2017). The loading of assimilates from the flag leaf is also disturbed under HS. Wheat showed optimum photosynthetic rates at 20-30 °C. The increase in temperature above 30 °C leads to significant reduction in photosynthesis and loading of assimilates from the flag leaf to the reproductive organs (Wardlaw 1974). HS reduces the displacement of water soluble carbohydrates from stem to grain, and results in a significant reduction in the final yield (Vignjevic et al. 2015). In conclusion, HS reduces the capabilities of source and sink, resulting in a substantial reduction in the final yield and quality.

Heat stress effects on respiration

Respiration significantly increases at increasing temperature, reaching a maximum at 40-50 °C. However, above 50 °C respiration considerably decreases owing to damage to respiratory mechanisms (Byrla et al. 2001). HS increases the respiratory carbon losses, reduces ATP

production and increases ROS production (Huang et al. 2012). The respiration in wheat flag leaf significantly increased under HS, leading to significant decline in photosynthesis and lower production (Almeselmani et al. 2012). HS negatively affects the CO_2 and O_2 solubility, and kinetics of Rubisco (Cossani and Reynolds 2012). HS significantly increases the O_2 *vs*. CO_2 solubility in plant leaves, which substantially reduces the efficiency of CO_2-concentrating mechanisms (Li and Liu 2007). Rubisco is the prominent enzyme that catalyzes photosynthesis and photo-respiration, whose rates depend on the respective carboxylase and oxygenase activities of this enzyme (Laing et al. 1974). At HT, the mesophyll concentration of CO_2 is the major limiting factor to carboxylase activity. HS reduces the photo-synthetic efficiency owing to CO_2 loss as a result of photo-respiration (Jordan and Ogren 1984). Under HS, the oxygenation takes over the carboxylation by the formation of phosphor-glycolate, which needs to be re-converted into phosphor-glycerate by CO_2 loss. Moreover, increase in oxygenase activity of Rubisco significantly limits photo-synthesis in C_3 plants by photo-respiration (Sharkey 1988). Additionally, HS reduces photosynthesis due to lower production of Rubisco, which is due to reduction in enzymatic activities and damages at the electron transport system in the PS-II (Salvucci and Crafts-Brandner 2004b). Lastly, at HT, CO_2 diffusion significantly decreases owing to increase in temperature sensitivity of photosynthesis, thus leading to increase in photo-respiration (Sun et al. 2013).

Heat stress induced oxidative damage

Like other abiotic stresses, HS also results in the accumulation of unwanted and harmful ROS species, i.e., hydrogen peroxide (H_2O_2), hydroxyl radical ($^·OH$) and super oxide ($^·O_2^-$), which are responsible for production of oxidative stress in plants (Asada 2006). ROS mainly originate from

14

reaction centers of PS-I and PS-II. However, other plant organelles, i.e., mitochondria and peroxisomes, contribute to ROS production (Soliman et al. 2011).

A linear relationship has been found between PS-II maximum efficiency and ROS accumulation in plants, due to HT damage to photosystems leading to lower absorption of photons (Halliwell 2006). Under HS conditions, when PS-I and PS-II are saturated by incoming photons, the photons in excess with respect to those required for CO_2 assimilation become the source of ROS (Halliwell 2006). Among ROS, $^{.}O_2^{-}$ is produced by the photo-oxidation reaction (flavour-protein, redox cycling), through Mehler reaction in plant chloroplast, during the mitochondrial ETCs reactions and glyoxisomal photo-respiration, by NADPH oxidase in plasma membrane, xanthine oxidase and membrane polypeptide. Additionally, $^{.}OH$ is produced as the reaction of H_2O_2 with O_2 and $^{.}O_2^{-}$ in photo inhibition transferring of electrons of PS-II in the chloroplasts (Savicka et al. 2010; Bavita et al. 2012).

The ROS cause various types of physiological disorders in plants. For instance, $^{.}OH$ radicals react with the photosynthetic pigments, proteins, lipids, DNA and even all cell constituents (Moller 2007). $^{.}O_2^{-}$ oxidizes proteins, unsaturates fatty acids and plant DNA (Karuppanapandian et al. 2011). ROS also reduce the permeability of membranes, de-nature plant proteins and cause lipid per-oxidation (Camejo et al. 2006; Halliwell 2006). A significant reduction in photo-synthetic light reactions has been reported even under moderate HS, owing to increase in electron leakage from the thylakoid membranes as a results of ROS accumulation (Bavita et al. 2012; Savicka et al. 2010). HS also increases leaf temperature, which in turn reduces the activities of enzymatic anti-oxidants and considerably increases the malondialdehyde (MDA) contents in plant leaves (Hurkman et al. 2009; Mohammed and Tarpley 2010). The exposure of wheat seedlings to HS led

to significant increase in MDA at early growth stages; moreover, MDA contents were further increased during later growth stages (Miller et al. 2009).

ROS also degrade and breakdown the polymeric proteins into soluble forms, resulting in early leaf senescence (Young et al. 2004). The prolonged high temperature also results in accretion of ROS at the outer surfaces of plant plasma membranes, in turn leading to depolarization of membranes (Qi et al. 2010) and activation of Ca-induced respiratory burst oxidase homolog D. Under such conditions, ROS accumulated in cells can activate programmed cell death (Qi et al. 2010).

Heat stress effects on reproduction

All the plant tissues and development stages are sensitive to HS. However, reproduction is most sensitive to HS and a few degree increase in temperature during flowering can significantly decrease the final yield (Lobell et al. 2011b). A brief HS period at the onset of the reproductive stage can reduce the floral buds and cause flower abortion. However, the extent of this depends on plans species and genotype (Sato et al. 2006). HS at the early reproductive stage results in no flower leading to no seed or fruit setting (Maheswari et al. 2012). HS also impairs meiosis in sex organs (male and female), and curbs germination of pollen, growth of pollen tube and viability of ovules, resulting in significant increase in sterility. Higher temperature at reproductive stage also decreases the number of pollen grains retained by the stigma, and endosperm and pro-embryo growth. All these factors together are responsible for increased sterility and consequent reduction in final yield (Cao et al. 2008).

Heat stress (33 °C) at plant heading in wheat reduced anther dehiscence and pollen fertility, leading to reduction in quantity of pollens on plant stigma and, consequently, decline in ovule fertilization and significant reduction in seed production (Ahamed et al. 2010). HT (> 35 °C) actually increased

sterility of pollen and reduced its germination and consequently the seed yield in maize (Suwa et al. 2010). Genotype variability within a species plays a role in sensitivity to HT (Hurkman et al. 2009).

Additionally, HT causes a significant increase in ethylene production resulting in male sterility of pollen. The production of ethylene also inhibits the enzymes involved in sugar-starch metabolism, weakening the sink strength, i.e. constraining grain filling with the final result of grain sterility. HT at reproductive stages decreases ear length, spikelet and fertile floret numbers, and leads to reduction in grain yield (Prasad et al. 2008a). HS at flowering stage is considered more noxious that at grain filling stage (Zhang et al. 2013). HS also increases flower and fruit abortion and abscission, and thus leads to reduction in seed/fruit production (Tubiello et al. 2007; Tan et al. 2011).

Morphological mechanisms of heat tolerance

Avoidance

Plants own various mechanisms enabling them to withstand HS under two time frames: short term avoidance or acclimation, and long term phenological and morphological changes. The short term mechanisms include leaf rolling or change in leaf position and lipidic membrane composition, and cooling as the result of transpiration. Long term morphological changes in response to HS include increased density of leaf stomata and hair, and larger vessels (Srivastava et al. 2012). Some crops mature earlier under HT, which leads to small yield losses and is an important escape mechanism in plant ecology (Adams et al. 2001). Plants growing in hot climates also have the ability to reduce light absorption thanks to small hairs on leaf blade that work as protective cover ensuring plant survival. Leaf rolling is another important adaption: plants roll leaf blade in parallel to sun rays,

thus reducing the absorption of solar radiations. Plants with smaller leaves more easily avoid the HS compared to plants with larger leaves. Small leaves disperse the heat to external environment more rapidly due to lower resistance of air boundary layer, compared to larger leaves.

Plants have some other mechanisms, e.g., intensive transpiration that lowers leaf temperature up to 6-10 °C and therefore, prevents HS (Fitter and Hay 2002). HS also determines leaf rolling that is a way to increase water leaf use efficiency (Sarieva et al. 2010). Plants are highly sensitive to HS during the active growth stages. However, some selected plants as bulbous barley (*Hordeum* spp.) and cocksfoot (*Dactylis glomerata* L.) increase their resistance in summer while others as lucerne (*Medicago sativa* L.) and potato (*Solanum tuberosum* L.) show higher tolerance during winter dormancy (Fitter and Hay 2002). It has been reported that dormant plants become more resistant to HS than non-dormant plants on the arrival of HS. There is a close relationship between drought and HS, and the consequences of either stress on plants are difficult to distinguish. Therefore, plants must be adapted to avoid both heat and drought stress (Fitter and Hay 2002).

Phenotypic flexibility

Plants also have some phenotypic flexibility under HS, which is also similar to that under drought stress. Generally, plants reduce their size, close stomata, reduce water loss, and increase the xylem vessels in roots and shoots (Anon et al. 2004). HS increases membrane permeability and damages mesophyll cells (Zhang et al. 2005). Some species also produce polymorphic leaves at the onset of HS, and decrease water loss owing to the bi-modal behaviour of stomata (Sayed 1996). Plants also undergo modifications at sub cellular levels under HS, as substantial changes in structural organization of thylakoids, which significantly affect photosynthesis (Karim et al. 1997).

Additionally, under HS mesophyll cells become round shaped, stroma lamellae swollen, vacuole contents clustered, and mitochondria get empty (Zhang et al. 2005). All these changes lead to antenna depletion of PS-II and therefore, reduce the activities of photosynthesis and respiration (Zhang et al. 2005). Changes in HS generally occur at both cellular and sub-cellular level, resulting in stunted growth and poor production.

Phenological changes

Plants act remarkable phenological changes to withstand HS, and their sensitivity to HS depends on growth stages. However, this still depends on species and genotype, as in many other factors of HS (Howarth 2005). The development stage at which HS occurs determines the severity of the ensuing damage. However, it is still unclear if the detrimental effects of all HT episodes at all growth stages are cumulative or not (Wollenweber et al. 2003). All the vegetative as well as reproductive stages may be affected. HS during the vegetative stages undermines gas exchange activities, while at reproductive stages, a rapid arrival of HS leads to flower abortion and lower seed production. However, this effect is still variable among species (Young et al. 2004). Some plants have early heading, which is an advantage owing to a higher retention of green leaves at anthesis, resulting in lower yield loss (Tewolde et al. 2006). Consequently, it is imperative to detect growth stages and processes that are sensitive to HS, to determine the heat tolerance potential of plants.

Tolerance mechanisms

Heat stress tolerance that refers to the ability of crop plants to grow and produce economically under HS, is a special plant trait. It varies among species, and even within the same plant organs

and tissues. Plants own various mechanisms ensuring their survival under HS. There are short term

mechanisms, i.e., avoidance and acclimation, and long term evolutionary mechanisms.

Plants have major tolerance mechanisms, i.e., ion transport, abundance of late embryogenesis

proteins, presence of osmo-protectants, and anti-oxidant defense system (Rodríguez et al. 2005).

Plants also change leaf orientation, perform intensive transpiration cooling, and change the lipid

composition of membranes to ensure survival under HS (Rodríguez et al. 2005; Radin et al. 1994).

Plant tissues show significant variations in their exposures and responses to HS (Queitsch et al.

2000). Plants have ionic and osmotic adjustment, change membrane permeability in response to

HS, protect and repair the proteins and cell membranes damaged by HS (Vinocur and Altman

2005).

Physiological mechanisms of heat tolerance

Waters relations

Plants maintain a consistent water status under non-limiting water supply regardless of

temperature; nonetheless, HT impairs plant ability to maintain tissue water status under limiting

water supply (Mazorra et al. 2002). Insufficient water supply mostly occurs in field conditions;

under these conditions HT reduces plant ability to maintain tissue water status (Simoes-Araujo et

al. 2003). High temperature at night time reduced the leaf water potential of *Lotus creticus* (L.)

plants grown under water limiting conditions (Anon et al. 2004). In sugarcane, leaf water potential

changed considerably even under optimum water supply, indicating the influence of HS on the

hydraulic conductance of roots (Wahid and Close 2007). Likewise, in tomato it was observed that

HS leads to significant reduction in plant water relations and hydraulic conductance of roots

(Morales et al. 2003). The maintenance of tissue water status during stress conditions upkeeps

physiological processes and ensures plant survival under HS. Nonetheless, HT during day time increases transpiration, induces water deficiency and disturbs plant physiological processes (Tsukaguchi et al. 2003).

Osmolyte accumulation

Plants accumulate a variety of low molecular mass compounds under HS in order to increase their survival. These low molecular weight substances are known as osmolytes (Sakamoto and Murata 2002). Plants accumulate different osmolytes under high temperature, e.g., sugars, proline, ammonium and sulphonium compounds (Sairam and Tyagi 2004). The accumulation of osmolytes increases plant survival under stress conditions, by protecting the cellular structure, and is considered a central dogma in plant stress physiology (Hare et al. 1998).

Glycine-betaine (GB) is an important osmolyte whose concentration increases under various abiotic stresses (Sakamoto and Murata 2002). However, GB synthesis varies among species and genotypes (Ashraf and Foolad 2007). For instance, a higher GB synthesis was observed in maize as compared to sugarcane (Wahid and Close 2007). Conversely, some plant species, e.g., rice, mustard (*Sinapis* spp.), tobacco (*Nicotiana tobacum* L.) and *Arabidopsis thaliana* (L.) Heynh. cannot synthesize GB naturally under stress conditions,. To close this gap, genetic engineering has introduced the bio-synthetic pathways for GB in GB-deficient plants (Sakamoto and Murata 2002; Quan et al. 2004). Plants also accumulate proline under HS conditions (Kavi-Kishore et al. 2005), and both GB and proline buffer the cellular redox potential under HT conditions (Wahid and Close 2007). Likewise, sugars accumulate under HS, providing greater implication for HS tolerance (Wahid and Close 2007). HS disrupted the sugar metabolism and proline transport during reproductive stage, and thus reduced the fruit setting in tomato (Sato et al. 2006). In conclusion,

21

osmolytes perform significant roles in the deployment of HS tolerance, and their accumulation can be increased in plants through breeding approaches, genetic engineering and marker assisted selection (Ashraf and Foolad 2007).

Cell membrane thermostability

Heat stress substantially reduces membrane permeability and leads to significant alterations in photosynthesis and respiration. The sustained functions of cell membrane under HS are important for the process of photosynthesis and respiration (Blum 1988). HS augments kinetic energy and accelerates the movements of various molecules athwart the plant membranes that, consequently, lose the chemical bindings among their molecules. HS denatures proteins and increases the concentration of unsaturated fatty acids, and therefore, makes membranes more fluid and porous (Savchenko et al. 2002). Membrane biological functions and integrity are severely affected by HS that affects the structure (tertiary and quaternary) of membrane proteins and increases membrane permeability and electrolyte leakage. The increase in electrolyte leakage decreases membrane thermo-stability in different crop plants as barley (*Hordeum vulgare* L.), cotton (*Gossypium* spp.), sorghum and cowpea (*Vigna unguiculata* L.) (Wahid and Shabbir 2005; Wahid et al. 2007). The electrolyte leakage in plants varies among tissues, organs, growth stages, and depending on the growing season. For instance, in the maize crop, injure to plasma-lemma owing to heat was more severe in older than younger leaves (Karim et al. 1999). In sugarcane, the concentration of saturated fatty acids increased under HS, as consequence of elevated leaf temperatures reducing plant heat tolerance (Wahid et al. 2007). Likewise, in *Arabidopsis* it was reported that under HS the total lipid content of membrane decreased by more than 50%, and the ratio of unsaturated to saturated fatty acids decreased by 30% (Somerville and Browse 1991). Both circumstances are

22

conductive to reduction in heat tolerance. However, in some other species it was observed that lipid saturation cannot be correlated with heat tolerance, suggesting that other factors may be limiting for crop growth, rather than reduction in membrane stability. The relationships between crop yield and cell membrane thermo-stability (CMT) varies among species and even within the same species. For instance, a significant positive association was noticed between CMT and final grain yield in sorghum (Sullivan and Ross 1979), whereas no relationship was recorded between yield and CMT in wheat (Shanahan et al. 1990).

Hormonal changes

Plant hormones play a significant role in plant behaviour under stress conditions. Cross-talk in hormonal signaling is the basis for plant ability to retrieve multiple inputs and respond appropriately. HS clearly influences hormone synthesis and degradation, and allocation to diverse plant organs (Maestri et al. 2002). Ethylene (C_2H_4) and Abscisic acid (ABA) are plant stress hormones that regulate various physiological processes acting as the signal molecules. It is generally acknowledged that under HS the level of ABA considerably increases. However, the level of ABA did not increase under HS in bentgrass (*Agrostis stolonifera* L.), although it was accumulated when plant recovered from the stress, which gives an evidence of its role during the late stress phase (Larkindale and Huang 2005). ABA changes gene expression, modulates the up and down regulations of different genes, and improves plant acclimation and adaptation under HS (Swamy and Smith 1999; Xiong et al. 2002). ABA also leads to induction of several heat shock proteins (HSP), which improve plant heat tolerance (Pareek et al. 1998; Rojas et al. 1999).

Ethylene, too, regulates several processes in plants, i.e., germination, flowering, fruiting and plant tolerance to stress conditions. HS alters C_2H_4 concentration in plant species (Arshad and

23

Frankenberger 2002). For instance, the concentration of C_2H_4 was significantly inhibited in wheat at 35 °C; in soybean it was increased up to 40 °C, but it was severely inhibited when temperature rose to 45 °C. In kiwifruit, HT up to 35 °C increased the C_2H_4 concentration significantly, whereas temperature above 35 °C significantly inhibited C_2H_4 production (Antunes and Sfakiotakis 2000). In maize, it was noticed that C_2H_4 was maximum and minimum at the top and middle of the ear, respectively. A major role is, thereby, evinced for C_2H_4 in assimilate partitioning at grain filling (Fenglu et al. 1997). C_2H_4 is assumed to counter the inhibitory effects of HS by increasing the activities of mannanase, which improves the seed germination by breaking the endosperm (Nascimento et al. 2004).

Salicylic acid (SA) is an imperative hormone involved in plant response to HS. It participates in the signaling pathway referred to the systemic acquired resistance (SAR), and the hyper-sensitive responses (HR) (Kawano et al. 1998). SA induces HS tolerance through involvement in both Ca^{2+} homeostasis and antioxidant system (Wang and Li 2006b).

Sulpho-salicylic acid (SSA) is the imitative of SA that removes a large part of H_2O_2 and increases plant ability to withstand HS. Cucumber seedlings treated with SSA showed an increase in catalase (CAT) activity that effectively removed H_2O_2 (Shi et al. 2006). The activities of glutathione peroxidase (GPX), ascorbate peroxidase (APX) and glutathione reductase (GR) were also increased, but they did not effectively remove H_2O_2. The other derivatives of SA, i.e., cetyl-SA and methyl salicylate (MeSA) have additional functions (Dat et al. 1998). They also act as signaling molecules, and enhance HS tolerance in the holm oak by increasing xanthophyll de-epoxidation, and the leaf concentrations of ascorbate, anti-oxidants and tocopherol (Wang and Li 2006a).

Gibberellins (GA) and cytokinins also have a substantial role in heat tolerance. For instance, exogenously applied GA impaired GA synthesis and significant improved heat tolerance in wheat (Vettakkorumakankav et al. 1999). In bentgrass, the level of cytokinins decreased in the roots and shoots in association with the reduction in dry matter production (Liu and Huang 2005). Moreover, Banowetz et al. (1999) found that the reduction in cytokinins owing to HS in wheat was responsible for the decrease in kernel filling and final dry weight (Banowetz et al. 1999). Brassinosteroids were also discovered as important hormones to increase HS tolerance in tomato and *Brassica* species, but not in cereals (Dhaubhadel et al. 1999). However, their role needs to be further explored.

Secondary metabolites

Secondary metabolites (SM) also play a significant role in plant survival under HS conditions. SM synthesis is based on intermediates of the primary carbon metabolism via shikimate, phenylpropanoid and mevalonate pathways (Wahid and Ghazanfar 2006). HS normally induces the production of different phenolic compounds, i.e., flavonoids and phenylpropanoids. HS increased the synthesis of phenolics and overpowered their oxidation, which increased the acclimation of watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) against HS (Rivero et al. 2001). Carotenoids are important SM protecting cell structures against different abiotic stresses (Wahid 2007). For instance, xanthophyll cycle plays an indispensable role in photo-protection; as zeaxanthin, it has a hydrophobic nature, and is located at the periphery of the light harvesting complex to protect the membrane lipids from the oxidative damages caused by HS (Horton 2002). It has been widely documented in the literature that carotenoids stabilize and protect the lipidic

component of thylakoid membranes (Velikova et al. 2005). The accumulation of xanthophyll

decreases the fluidity of membranes and vulnerability to lipid per-oxidation (Havaux 1998).

Phenolics include different compounds, among which flavonoids, anthocyanins, lignin are most

important SM playing several roles also related to HS tolerance (Chalker-Scott 2002; Wahid

2007). The accumulation of phenolics under HT increases the amount of phenyl-ammonia-lyase

(PAL) enzyme and the activities of peroxidase and polyphenol-lyase (Rivero et al. 2001).

Anthocyanins are an important subclass of the flavonoids being modulated in plant tissues under

HT. HT decreased their concentration, while low temperature increased their concentration in fruit

and bud of aster (*A. ericoides* × *A. pilosus*) (Sachray et al. 2002). The lower anthocyanin

concentration in plants under HT is associated with reduction in their synthesis and stability

(Sachray et al. 2002). Conversely, a significant increase in the accumulation of anthocyanins was

observed in few plants as sugarcane, where it induced HS tolerance (Wahid and Ghazanfar 2006).

Anthocyanins also decreased the leaf water potential, which in turn increased the water uptake and

reduced the transpirational losses under HT (Chalker-Scott 2002).

Isoprenoids are also an important class of SM that are synthesized in plants by the mevalonate

pathway (Taiz and Zeiger 2006). Isoprenoids are low molecular weight compounds, whose

emission from plant leaves induces HS tolerance in the photosynthetic apparatus (Loreto et al.

1998). Some other authors reported that bio-synthesis of isoprenoids is cost effective, and their

bio-synthesis induces HS stress tolerance (Funk et al. 2004). Plants with good ability to emit high

amounts of isoprenoids denote best photosynthetic performance under HS (Velikova and Loreto

2005). Moreover, isoprenoids also protect the PS-II from ROS damages, and prevent the

membrane from reacting with ROS, namely the singlet oxygen, by means of isoprene-conjugated

26

double bond (Velikova et al. 2005). In conclusion, plants accumulate a wide range of SM that ensure their survival under HS through various kinds of modifications.

Molecular mechanisms of heat tolerance

Oxidative stress and antioxidants

Beside tissue dehydration, HS also triggers oxidative stress in plants, which is associated with the production of ROS. However, plants have different enzymatic and non-enzymatic anti-oxidant systems to scavenge these ROS (Sairam and Tyagi 2004). The activities of anti-oxidants considerably increase under HS, thus protecting plants from the damaging effects of HS (Babu and Devraj 2008).

For instance, increase in the expression of superoxide dismutase (SOD) under HS removes the H_2O_2, and affects the oxidation of toxic reductants, lignin bio-synthesis in cell wall, auxin metabolism, plant response to wounding and insect attack, and different respiratory processes (Scandalios 1993). Moreover, APX expression is associated to different physiological injuries caused by HS (Mazorra et al. 2002). The reduction in anti-oxidant activities under HS contributes to mitigate these injuries in plants (Fadzillah et al. 1996). The increase in activities of ascorbate and glutathione reduced the ROS in turfgrass species (Xu et al. 2006).

Activity of anti-oxidant enzymes is sensitive to temperature, i.e., their activation occurs at varying temperature. However, Chakrabortty and Pradhan (2011) noted that CAT, APX and SOD activities showed an initial increase followed by a decline at temperature up to 50 °C, whereas peroxidase (POX) and GR activities considerably decreased across the range of temperatures from 20 to 50 °C. Additionally, it was observed that activities of anti-oxidant enzymes was maximum at 35-40

27

°C, although this also depended upon crop HS tolerance, growing season and growth stages (Chakraborty and Pradhan 2011).

The increase in the synthesis of ascorbate (AsA) and glutathione (GSH) in turfgrass species reduced the production of ROS (Xu et al. 2006). Likewise, in the wheat crop it was noted that HS increased GSH accumulation and enhanced the enzymatic activities involved in GSH synthesis (Kocsy et al. 2002). Still in wheat, Balla et al. (2009) noticed a remarkable improvement in APX, CAT and glutathione *S*-transferase (GST) activities that induced HS tolerance by lowering ROS production. Almeselmani et al. (2009) noticed that anti-oxidants play a significant role associated with a considerable increase in CAT, APX, SOD, GR and POX activities at all growth stages in a HS tolerant wheat cultivar (C-306). Conversely, they noticed a significant reduction in these activities in a HS susceptible cultivar (PBW 343). Rani et al. (2013) noticed that activities of SOD, POD, CAT and APX were significantly higher in a tolerant cultivar of Indian mustard (*Brassica juncea* (L.) Czern.), compared to a susceptible cultivar. Moreover, they also reported that, under HS conditions, SOD and POX activities were decreased, whereas APX activity continuously increased from beginning to end in both cultivars.

Kumar et al. (2012b) exposed maize and rice plants to HS, and noticed that the expression of enzymatic (CAT, APX and GR), and non-enzymatic anti-oxidants (GSH, AsA) was significantly higher in maize than rice. However, no variation was observed between maize and rice for SOD activity. Since maize, a C_4 plant, has an intrinsically higher tolerance to HS than rice, a C_3 plant, these observations evidence the different sensitivity of these two groups to HS. Likewise, Hasanuzzaman et al. (2011) exposed wheat seedlings to HS (38 °C), and observed an increase in enzymatic and non-enzymatic anti-oxidant activity. In conclusion, an increase in temperature significantly increases the expression of anti-oxidants that induce HS tolerance in plants. However,

28

in tolerant cultivars a higher expression of anti-oxidants is shown, compared to heat susceptible

cultivars.

Heat shock proteins

In response to HS, plants have the ability to produce heat shock protein (HSPs), which induce HS

tolerance in plants and therefore, improve their performance under HS. The production of HPSs

increases following sharp as well as gradual increases of temperature (Schoffl et al. 1999). The

increase in HSPs under HS is a general occurrence in plants, humans and even bacteria (Vierling

1991). In higher plants, HSPs are produced at any growth stage in response to HS. The majority

of the HSPs are homologous among organisms (Vierling 1991). Three classes of HSPs have been

identified on the basis of molecular weight: HSP-70 and HSP-90, and lower molecular weight

proteins of 15-30 kDa. However, the proportions of the three classes can significantly vary among

plant species. The HSP-70 and HSP-90 are expected to increase by 10 folds under HS, whereas

the lower molecular weight proteins increase by 200 folds under HS (Feussner et al. 1997).

Generally, HSPs are associated with specific cell structures, i.e., cell walls, chloroplasts,

ribosomes, and mitochondria (Yang et al. 2006). Korotaeva et al. (2001) exposed rye (*Secale

cereale* L.), wheat and maize seedlings to HS (42 °C). They noted that five lower molecular weight

mitochondrial proteins (19, 20, 22, 23 and 28 kDa) were expressed in maize, but only one (20 kDa)

was expressed in rye and wheat, indicating a higher heat tolerance in maize. Likewise, heat

tolerance in maize showed an increase in the expression of HSPs, compared to heat susceptible

lines (Moriarty et al. 2002).

The expression of HSPs under HS protects the machinery of protein bio-synthesis

(Miroshnichenko et al. 2005). HSPs also prevent protein denaturation caused by HS. It has been

reported that the state of aggregation and the structural conformations of small HSPs are crucial for their functions of heat tolerance in plants (Iba 2002). Small HSPs can gather into heat shock granules (HSGs) and subsequently dis-assemble, which is a prerequisite for plant survival under HS (Miroshnichenko et al. 2005).

Additionally, some other proteins have been identified in plants, in response to HS. HSP68 is a low molecular weight protein localized in cell mitochondria, whose expression has been reported in the barley, maize, tomato and soybean crop (Neumann et al. 1993). HSP101 is also an important HSP that promotes the renaturation of proteins under HS. The expression of HSP101 varies among plant tissues: in maize Young et al. (2001) noticed the maximum HSP101 expression in tassel, ears, embryo and endosperm, compared to root, leaf and floral region. There is a significant difference among plant species and genotypes for the production of HSPs (Wood et al. 1998). The accumulation of HSPs protects the cell apparatus from HS. In some plants, roots also synthesize HSPs that improve plant ability to cope with HS by ameliorating the working efficiency of roots (Nieto-Sotelo et al. 2002).

The mechanisms underlying HS tolerance in plants are still unclear. Many authors have reported that HSPs ensure the stability and functioning of proteins under HS (Fig. 3). Moreover, HSPs also fold the de-natured proteins into proper shapes for their normal functioning (Bowen et al. 2002). HSPs also help protein displacement across compartments, and promote the transport of older proteins to sites of disposal inside the plant. HSPs also support protein translation and translocation, perform proteolysis and protein folding, and re-activate denatured proteins (Fig. 3) (Zhang et al. 2005). Moreover HSPs protect the PS-II from the oxidative stress (Neta-Sharir et al. 2005), and participate in ATP dependent reactions for the unfolding of proteins, preventing their

denaturation (Iba 2002). Additionally, HSPs maintain membrane permeability and protect the PS-II from adverse effects of HS (Barua et al. 2003).

Fig 3 has to be placed here

Beside HSPs, plants synthesize other proteins as ubiquitin, cytosolic Cu/Zn-SOD and Mn-POD (Sun and Callis 1997), whose expression significantly increases HS tolerance: a significant improvement in the expression of ubiquitin was recorded in soybean under HS (Ortiz and Cardemil 2001). Khanna-Chopra and Sabarinath (2004) noticed small fractions of Cu/Zn-SoD protecting plants from HS by maintaining the stability of chloroplasts. Late embryogenesis abundant (LEA) proteins are also important proteins produced under HS conditions. They protect the citrate synthase from desiccation under HS (Goyal et al. 2005). Majoul et al. (2003) noticed a significant increase in expression of 25 LEA proteins in wheat during late grain filling stage. Recently, some important lower molecular weight proteins, dehydrins, were identified in sugarcane, and their expression was significantly increased at HS onset (Wahid and Close 2007).

Strategies to mitigate heat stress

Conventional breeding strategies

Conventional breeding strategies based on genotype selection and inter-mating result in scarcity of genetic variation for characters that underwent domestication and selection (Gur and Zamir 2004; McCouch 2004). Thus, improvement in crop performance under stress conditions needs extensive research to sort out the genetic variability in wild and cultivated plant species. Physiological and genetic inquiries provide a clear cut indication: genetic traits associated with abiotic stress tolerance are very complex, as they have a polygenic control and are highly sensitive to environmental conditions (Blum 1988). Moreover, HS tolerant genes and quantitative trait loci

(QTLs) must be explored within non-adapted genotypes and wild land races in order to improve

HS tolerance in plants (Fernie et al. 2006). Impressive results have been reported in describing the

genetic variation for HS. Additional efforts have been made to introduce heat tolerant genes in rice

genotypes (Jiang-lin et al. 2011).

However, the quantification of tolerance in species results in serious problems. For instance, under

field conditions direct selection is very difficult owing to uncontrolled environmental conditions

significantly affecting the accuracy, precision and repetition of trials. Moreover, HT conditions

cannot be granted in the field, and HS may occur or not. Since HS is a stage specific occurrence,

HS tolerance at a specific growth stage cannot be correlated with that at another stage. Therefore,

individual stages of plant growth must be evaluated for HS tolerance, and individual growth stages

must also be properly evaluated to identify and characterize the genetic variation of tolerance

components. Several circumstances as the low heritability and a wide network of minor and major

QTLs undercut the possibilities of direct selection for improving crop behaviour under HS

conditions (Manavalan et al. 2009).

Environmental and composite hurdles hinder the obtainment of lines with best performance under

HS. Poor understanding of the inheritance of HS associated with poor availability of the QTLs for

HS further constrain the progress in crop amelioration (Cossani and Reynolds 2012). The genetic

tailoring of important physiological traits can be an effective strategy to incorporate the QTLs that

determine multifaceted HS tolerance in crop plants (Fig. 4), in accordance with the scheme

proposed for drought tolerance (Farooq et al. 2009a). Breeding strategies relying on physiological

traits have a competitive edge over conventional breeding approaches (Reynolds and Trethown

2007). Moreover, physiological approaches increase the profitability of added genes under adverse

conditions (Reynolds and Trethown 2007). Breeding techniques must be aimed at various

32

physiological traits that are related to structure of plant canopy for HT acclimation (Table 4), delay in senescence, improved photosynthetic efficiency, reduced respiration, improved harvest index and reproductive traits (Cossani and Reynolds 2012; Gupta et al. 2012). Therefore, physiological trait-based breeding is an important strategy to develop HS tolerant cultivars without compromising yield (Table 4).

Fig 4 has to be placed here

Molecular and biotechnological approaches

Molecular biology and molecular markers are the imperative field and techniques, respectively, to identify HS related QTLs (Maestri et al. 2002). Biotechnology played a significant role, recently, in identifying heat tolerant genes in crops including tomato and maize, where different genes were actually identified to be responsible for HSP synthesis (Momcilovic and Ristic 2007). Moreover, HS tolerance in plants can be regulated by variations in the activities of transcription and translation. Transcription is necessary during the stress period in order to support the translational activities required (Gallie and Pitto 1996). Generally, such activities in plants change quickly during seed germination, and similarly, during the heat and drought stress (Gallie et al. 1998).

Two biotechnological strategies are generally used to improve HS tolerance in plants: genetic transformation, and marker assisted selection (MAS) (Fig. 4). Both techniques have significantly contributed to understanding the genetic and bio-chemical bases of plant HS tolerance, as premise for the development of HS tolerant genotypes (Fig. 4). MAS is an imperative technique to improve HS tolerance in plants owing to complexity of HS, and difficulties in phenotypic selection for HS tolerance (Foolad 2005). However, the use of MAS implies the identification of proper genetic markers that are linked with QTLs/genes responsible for HS tolerance at whole plant or individual

component level. Various genetic markers linked with the different abiotic stresses have been identified in several crops in the recent past. Use of this technology has substantially identified and characterized numerous QTLs with excellent impacts on the HS at diverse plant growth stages (Foolad 2005). More recent techniques, i.e., gene expression and genetic transformation have fostered a well understanding of bio-chemical and genetic bases of plant HS tolerance, as premise for breeding genotypes with stronger tolerance to HS. The changes in gene expression and production of targeted genes, proteins and different enzymes with the help of transgenic techniques have led to increases in HS tolerance in diverse plant species (Zhang et al. 2001; Rontein et al. 2002). In conclusion, biotechnological approaches are promising in view of developing HS tolerant cultivars. However, more research should be conducted in this field to understand physiological, molecular and genetic basis to develop cultivars with improved abilities to cope with the HS.

Table 4 has to be placed here

Omics approaches in developing heat stress tolerance

Omics are the newly developed techniques providing an opportunity to identify translational, transcriptional and post translational mechanisms, and the signaling pathways that appreciably regulate plants responses to HS (Hasanuzzaman et al. 2013). Omics also help in systematic examining and determining the correlations between the variations in the genomes, micromes, and proteomes of different plants in response to HT. Plenty of genes playing potential roles against HS have been identified using gene expression and genetic screens (Yeh et al. 2012).

Plants have the ability to regulate the post-transcription gene expression with the aid of non-proteic RNA, also called microRNAs (Chinnusamy et al. 2007). MicroRNAs play an important role in

micromics studies, helping to understand the mechanisms underlying HS tolerance in plants. Moreover, different microRNAs have been identified, which play an important role in plant accumulation of osmolytes in response to HS. MicroRNAs have different roles in plants; for example, stress down-regulated micro-RNA leads to accumulation of targeted RNAs and contributes to HS tolerance in plants, whereas stress up-regulated microRNA fails to target the specific RNAs and does not contribute to heat tolerance.

Moreover, the proper understanding of microRNA roles in cell tolerance, transcriptome homeostasis and developmental plasticity will help genetic engineering to develop HS tolerant cultivars. Microarray is a recently developed, important tool for analysis of the expression profiles of different genes induced by HS (Yeh et al. 2012; Liu et al. 2011). For example, transcripts of 170 cDANs from drought stressed plants with and without HS was reported in tobacco (Rizhsky et al. 2002). Many genes have been shown to be up regulated by a combination of heat and drought, not by either factor. Microarray investigations also increase acquaintance of different functions associated with HS tolerance. Recently, Rizhsky et al. (2004) investigated the genome array from *Arabidopsis* to study the transcript changes in response to HS, drought stress, and the two stresses combined. They noticed a 262% increase in transcript response to HS. Moreover, Penueli et al. (2003), with the help of microarrays noticed that HSPs are also expressed under other stresses, although expression of HSP ensues as consequence of HS. All these explanations suggest that omics approaches can be promising to develop genotypes with HS tolerance.

Planting time

Planting time is a non-monetary management option to get optimum yields under different HS conditions. The selection of suitable planting/sowing time avoids the HT during later growth

stages, i.e., anthesis and grain filling, which improves crop yield under HS. Moreover, crop growth and development vary with the sowing time, and selection of suitable sowing times is an important approach to get maximum yield under such adverse conditions (Radmehr et al. 2003; Turner 2004). Different authors reported maximum yield of wheat with early sowing, whereas later sowing leads to significant yield reduction owing to HS at later growth stages (Bassu et al. 2009; Bannayan et al. 2013). Delayed sowing reduces crop yield by negatively affecting crop yield components. In fact, delayed sowing leads to production of kernels with lower weight, lower productive tillers and thousand grain weight (Radmehr et al. 2003). Therefore, knowledge of proper sowing time in a specific area facing HT conditions is critical to achieve a good yield (Ortiz-Monasterio et al. 1994). Late sown crops face HT during the flowering and grain filling stages, which results in significant reduction of the final yield due to pollen sterility and lower grain filling (Farré et al. 2002; Robertson and Holland 2004). Moreover, late sowing also decreases the growth period and leaf area duration, resulting in rapid maturation (Ozer 2003). The increase in temperature during the late stages leads to different effects on seed quality and vigor. For instance, late sown soybean produced seeds with lower protein and oil contents, and seeds had less vigor compared to seeds obtained from the crop sown at optimum date.

Heat stress substantially reduces the rate of photosynthesis and increases ethylene production and therefore, triggers leaf senescence (Djanaguiraman and Prasad 2010). Proper sowing time allows plants to enjoy optimum weather conditions in view of maximum yield potential. Both sowing too early and too late can have devastating impacts on crop growth and productivity (Uzun et al. 2009). Likewise, late sown crops usually face the conditions of HT and high evapotranspiration during the reproductive stages, resulting in both heat and drought stress (Yau 2007). Therefore, to achieve the maximum yield potential crops should be sown at optimum time to avoid HT during later

growth stages; this strategy would significantly improve crop yield under the rising temperature scenario (Dordas et al. 2008; Nagarajan et al. 2010).

Nutrient management

Mineral nutrients play a significant role in final production. However, insufficient and unhinged supply of main nutrients, together with poor soil fertility, decrease crop production globally. It has been reported that more than 60% soils worldwide are nutrient deficient (Cakmak 2002). Therefore, adequate nutrient availability is necessary to achieve good yields. Optimum availability of nutrients maintains plant integrity by sustaining several physiological functions. N and Mg are important nutrients needed for the process of photosynthesis; P is a key component of nucleic acids, and required for energy production, while K is required for stomatal regulation and the activation of enzymes (Waraich et al. 2011; Hassan et al. 2017). Various authors have reported the beneficial roles of various nutrients against abiotic stresses; among them, Si and K are credited to improve crop salinity tolerance (Munns 2005; Tahir et al. 2011).

N plays an imperative role in carbon metabolism and utilization of absorbed light energy (Huang et al. 2004). However, N deficient plants feature an excess of unusable energy leading to oxidative damage. Moreover, N deficiency leads to lipid peroxidation under HS conditions (Huang et al. 2004). K deficiency reduces CO_2 fixation and impairs the partitioning and use of assimilates. Such changes lead to excess of photosynthetic electrons, in turn stimulating ROS production (Waraich et al. 2011). Mg is also an important nutrient for plants; small changes in Mg concentration affect chloroplast enzymes and lead to alteration in the photosynthetic process (Shaul 2002). Also Mg deficiency is shown to considerably decrease photosynthesis in plants under stress conditions (Hermans and Verbruggen 2005). Boron is an important micro-nutrient that substantially improves

the activity of the anti-oxidant system and alleviates the toxic effects of ROS produced by HS (Waraich et al. 2011). Mn also alleviates the adverse impact of HT by improved rate of photosynthesis and N metabolism in plants (Waraich et al. 2012). ROS are produced under both high and low temperatures conditions, and they have devastating impacts on plants (Srivalli and Khanna-Chopra 2004). Likewise, Selenium (Se) plays a structural role in GPX synthesis and therefore, protects plants from the negative effects of ROS (Lobanov et al. 2008). Being an important micronutrient, Zn substantially maintains membrane permeability, and optimum Zn supply protects plants from devastating impacts of HS (Alison and McDonald 2010). Ca is also required for activity of anti-oxidant enzymes (Jiang and Haung 2001); under HT, Ca requirement significantly increases to mitigate the negative effects of HS (Kleinhenz and Palta 2002). All these explanations suggest that adequate mineral nutrition is mandatory to maintain plant performance under stress in view of ensuring a good production.

Seed priming

Seed priming (SP) is a promising and economical approach being used globally to improve crop stand establishment (Farooq et al. 2009b). SP substantially improves seed germination, seedling emergence, crop stand and growth. SP using $CaCl_2$ and KCl significantly improves growth, dry matter production and crop yield components (Farooq et al. 2006). Seed priming of normal and low vigor seeds has been shown to improve root length, and root and shoot growth (Kausar et al. 2009; Moosavi et al. 2009).

Seed priming with various agents also improves crop performances under abiotic stresses including HS, drought and low temperate stress (Farooq et al. 2008). Likewise, SP led to optimum germination, better growth and early flowering, and resulted in maximum production under semi-

arid conditions in maize, rice and chickpea (*Cicer arietinum* L.) (Harris et al. 2001). SP led to early flowering (8-10 days), maturity (9-10 days), and reduced chances of HS occurrence at flowering, resulting in maximum yield of rice and wheat (Harris et al. 1999; Sattar et al. 2010).

Tomato seeds primed before sowing showed improved osmotic adjustment, stomatal conductance, plant growth and development under HT conditions (Morales et al. 2003). Similarly, the leaves of cool-season turfgrass species showed a higher membrane stability and lower lipid peroxidation under HS conditions with primed *vs.* unprimed seed (Xu et al. 2006). In another study, Wahid and Shabbir (2005) found that barley seeds primed with glycine-betaine (GB) under HS had a lower membrane damage and better photosynthetic rate, osmotic adjustment, root and shoot dry biomass as compared to unprimed seeds.

Seed priming enhanced cell division and growth of apical meristems, resulting in vigorous wheat growth (Shakirova et al. 2003). SP with different substances prevents the photosynthetic system from damages determined by HS, via improving the activities of the anti-oxidant system (Ananieva et al. 2004; Hui-Jie et al. 2011). Moreover, seed priming with *Calpurnia aurea* (Ait.) Benth. leaf extract neutralized the free radicals under HS conditions, increasing the concentration of photosynthetic pigments (Adedapo et al. 2008). Seed priming also maintains higher cell membrane stability, helping plants to maintain the water potential under HT conditions (Mahboob et al. 2018). Seed priming also improves the production of different metabolites (proline, GB), which maintain osmotic adjustment, relative water content, and stabilize the HSPs to secure the photosynthetic system (Ahmad and Hasan 2011; Wang et al. 2014). In addition, GB production protects Rubisco activase near thylakoids, preventing Rubisco inactivation owing to HT (Allakhverdiev et al. 2008). Additionally, SP substantially increases sugar concentration under HS (Wahid et al. 2007). The increased accumulation of sugars mitigates the damaging effects of HS by preserving the water

39

balance and osmotic adjustment, and by protecting the cellular structures (Farooq et al. 2008). Seed priming also favours the bio-synthesis of phenolics (Mahboob et al. 2018), which have the ability to act as hydrogen donors by detoxifying ROS in the stabilization of membranes (Rice-Evans 2001).

Spray of osmo-protectants

Osmo-protectants have been recently identified as important molecules that have beneficial effects on plants subjected to HS, as they substantially improve plant growth and the activity of anti-oxidants under HS conditions (Hasanuzzaman et al. 2011). In a study conducted on sugarcane, Rasheed et al. (2011) found that exogenously applied GB (20 mM) and proline (20mM) improved various physiological processes and anatomical features in heat stressed plants. They also noticed that application of GB and proline increased the concentration of K^+, Ca^{2+}, proline and sugar, therefore reducing the negative impacts of HS by improving membrane stability and activity of the anti-oxidant system. In another study, Kaushal et al. (2011) noticed that exogenously applied proline protects various enzymes of carbon metabolism and anti-oxidant systems, which are the basis for HS tolerance in chickpea. They also found that exogenous proline results in lower membrane injury, improved water potential and chlorophyll content under HS. Moreover, Kumar et al. (2012) reported that exogenously applied proline and GB upgrade the growth and yield of chickpea under HS. Likewise, Chhabra et al. (2009) noted that application of phyto-hormones induces heat tolerance in chickpea by improving anti-oxidant activity and membrane stability.

Salicylic acid (SA) is an important osmo-protectant that significantly improves crop performance under HS. Wang and Li (2006) found that SA spray decreases electrolyte leakage, increases the activity of anti-oxidant systems and therefore, induces HS tolerance in grapevine. Similarly, SA

induced heat tolerance in grapevine by reducing the effects of HS on PS-II, and maintaining the

activity of photosynthesis and Rubisco under HS (Wang et al. 2010).

Kumar et al. (2012c) studied the response of ABA on growth of chickpea seedlings under HS.

They found that exogenously applied ABA improves plant growth by increasing the concentration

of endogenous ABA. Similarly, these authors studied the effect of variable concentrations of 24-

epibrassinolide (24-EBL) on mustard behaviour under HS conditions: the exogenously applied 24-

EBL induced HS tolerance in mustard by improving the activities of the anti-oxidant system. Nitric

oxide (NO) is an important compound involved in various plant physiological processes, and

improves crop performance against the HS (Waraich et al. 2012). The exogenously applied NO

significantly alleviated the HS by decreasing ion leakage, and improving the activities of different

anti-oxidant enzymes (Song et al. 2006).

Polyamines (PAs) are another group of lower molecular weight compounds found in plants,

animals and bacteria (Alcázar et al. 2006). PAs significantly accumulate in plants under HS and

improve plant performance by increasing membrane stability and anti-oxidant enzyme activity

(Hussain et al. 2011). PAs regulate the photosynthetic apparatus, maintain membrane stability and

improve the photosynthetic efficiency under HS (Kusano et al. 2007). PAs also influence the

synthesis of HSPs that maintain cell integrity and membrane stability under HS (Königshofer et

al. 2002).

Hitherto, selenium is not considered an essential element for plants. However, it has proved his

role as relevant osmo-protectant under various stress conditions including HS. Djanaguiraman et

al. (2010) studied the role of Se on plant physiological activities, yield and its components in

sorghum under HS (40 °C). They noticed that HS substantially reduces the chlorophyll contents,

photosynthetic rate and activity of the anti- oxidant system. The reduction in activities of the anti-

oxidant system resulted in membrane damage and led to electrolyte leakage owing to production of ROS. However, they noticed that application of Se improves membrane permeability and activities of anti-oxidant system, and therefore, improves yield and its components under HS conditions. In conclusion, osmo-protectants improve the activities of the anti-oxidant system, photosynthetic efficiency, membrane permeability, and reduce the production of ROS. This all results in improved crop performance under HS conditions.

Bacterial seed treatment

The use of biological agents including bacteria and fungi could determine improved HS tolerance in crops (Raaijmakers et al. 2009). Plant growth promoting rhizo-bacteria (PGPR) exert beneficial effects on growth under HS conditions (Nain et al. 2010). Seed inoculation with rhizo-bacteria substantially increased HS tolerance in the wheat crop (Yang et al. 2009; Anderson and Habiger 2012). Likewise, in another study Abd-El-Daim et al. (2014) reported that seed treatments with *Bacillus* spp. and *Azospirillum* spp. improve the tolerance against the HS by reducing the production of ROS. Hitherto, a few work have been done to explore the effects of microbes to improve HS tolerance in plants. More studies need to be conducted to determine the effects of biological agents against HS, and the mechanisms lying behind HS alleviation through microbial treatments.

Soil moisture conservation

Soil moisture conservation is an important practice that could be viable for plant production under HS conditions. A continuous water supply is essential to sustain the duration and rate of grain filling, and final grain size. Soil moisture can be conserved through different ways as mulching

42

that is an imperative technique to maintain the moisture and thermal regime in the soil system. Straw mulching significantly saves soil moisture by reducing evaporation (Chen et al. 2007; Glab and Kulig 2008), ensuring higher productions under HS and water limited conditions (Chakraborty et al. 2008). Moreover, organic mulch saves soil moisture and improves water and nitrogen use efficiency, i.e. the overall plant performance (Singh et al. 2011).

Water management

Heat stress is generally associated with water scarcity. Therefore, water management is crucial to improve crop production under the HS. It has been observed that plants can easily cope with HS as long as they can transpire easily. Moreover, many field crops can easily withstand HT (up to 40 °C) with sufficient water supply, whereas insufficient water supply dehydrates plant leaves and leads to substantial reduction in the final yield. The reasons for the lower production at high temperature lies in the fact that water stressed plants try to save water by closing their stomata; as a result, evaporative cooling considerably diminishes, and without cooling, leaf temperature reaches up to 50 °C. At such HT, plant physiological processes are significant curbed, and all these changes lead to lower production.

Therefore, irrigation scheduling and water application by appropriate irrigation methods can be assumed as the good practice for water management. Irrigation scheduling according to the critical growth stages, water availability and environmental conditions enable to achieve the maximum production with additional benefits of mitigating the negative effects of HS. When water supply is limited, crop irrigation should be applied at an IW/CPE (irrigation water/cumulative pan evaporation) ratio of 0.75, whereas, with unlimited water supply this may be increased up to 1.2 from tiller to flowering in wheat to get maximum crop yield (Chaudhary and Kumar 1980). The

irrigation control system (ICS) based on the reference crop evapotranspiration to schedule irrigation clearly influences the crop yield and yield traits, as compared to the intelligent irrigation system (IIS), which utilizes evapotranspiration models based on different sensors to measure actual weather conditions, i.e., wind speed, rainfall, radiation and temperature, and calculates evapotranspiration automatically (Al-Ghobari et al. 2013). Similarly, the application of irrigation water can play a significant role in mitigating HS. However, all this depends upon the availability of water. As the water resources are continuously being limited globally, sometimes full irrigation becomes impossible. Therefore, the irrigation schedule based on water availability and critical crop stages can determine a significant effect on the final production under limited water supply (Zhang et al. 2002; Tahar et al. 2011). In conclusion, irrigation scheduling based on critical growth stage, efficient irrigation method, supply of extra amount of water (depending on water availability), and application of irrigation based on soil moisture improves crop productivity by mitigating the effects of HS.

Conclusions and future prospects

Heat stress is an incumbent catastrophe prone to curb agricultural production throughout the globe. Plants show a wide array of responses to HS, consisting in substantial changes in growth, morphology and functioning. Overall, HS has a potentially devastating impact on plant growth and development. However, reproductive growth is the major phase being affected by HS. Thus, the occurrence of HS during the reproductive stages (anthesis - seed filling) determines the most serious losses in final production. Additionally, HS causes noticeable impacts of different nature, including oxidative stress, damaged photosynthetic machinery, reduction in photosynthesis, ATP production and membrane permeability.

44

In contrast to this, a wide range of morphological, physiological and molecular mechanisms enable plant survival under HS. The physiological and molecular mechanisms are the imperative ones, because they can help the breeders to develop genotypes with superior heat tolerance. At present, the physiological mechanisms of HS are quite well understood, but deeper insights are needed in several fields, especially to better understand the physiological basis of assimilate partitioning from source to sink. The need for additional studies is also envisaged concerning the response of plant roots to HS, involving root-shoot signaling and consequent effects on water and nutrient uptake.

One of the major motives for the inscrutable nature of HS tolerance in plants is the dismemberment of a narrow range of genetic pools that do not provide sufficient information to explore HS tolerance in major world crops as wheat, rice, maize, cotton and soybean. Therefore, it is necessary to assess and test the wild relatives, and the accessions and genetic materials having strong tolerance against HS. Modern technologies, i.e., genetic engineering, molecular markers, genomics, QTLs appreciablly contribute to understand complex traits in plants. However, there is a wide room for further improvements. As the genotype × environment interactions are still modestly understood, candidate QTLs identified in a specific background may not always perform well in a different background. Similarly, the transgenic plants developed for HS tolerance may not perform well under field conditions, or their field performance is unpredictable. However, application of research findings requires further validation of developed genetic materials in farmers' fields. Moreover, climate change models that differ geographically will also help the breeders to identify and develop HS tolerant genotypes for specific environments. Furthermore, plant performance under HS can be improved by proper water and nutrient management, and foliar application of osmo-protectants.

Microbial seed treatments can also play a significant role in the reduction of HS negative effects. However, future studies are direly needed to understand the mechanisms lying behind heat tolerance in plants. All these efforts will surely help to mitigate the negative effects of HS, and contribute to improved plant productivity and food security under the current scenarios of climate change and global warming.

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Table 1

Wheat (*T aestivum* L.)		Rice (*O. sativa* L.)		Maize (*Z. mays* L.)		Soybean (*G. max* (L.) Merr.)	
Country	Reduction	Country	Reduction	Country	Reduction	Country	Reduction
USA	>4%	China	>1%	USA	>9%	USA	>6%
China	>2%	India	>5%	China	>7%	China	>2%
France	>5%	Vietnam	>3%	France	>1%	Paraguay	>3%
Russia	>7%	Indonesia	>1%	Brazil	>4%	Brazil	>4%
India	>8%	Bangladesh	>2%	India	>4%	Argentina	>0.5%

(Zhao et al. 2017)

Table 2

Crop	Temperature	Effects	Reference
Lentil (*Lens culinaris* Medik.)	30 °C	Reduction in membrane permeability, rate of photosynthesis and Rubisco activity, and increase in stomatal conductance	Sehgal et al. 2017
Olive (*Olea europaea* L.)	40 °C	Reduction in activities of Rubisco, stomatal conductance and carbon assimilation efficiency	Haworth et al. 2018
Wild barley (*Hordeum vulgare* L.)	42 °C	Inhibition of functionality and quantum efficiency of PS-II, and reduction in photo-synthetic rate	Jedmowski et al. 2015
Poplar (*Populus simonii* Carrière)	42 °C	Reduction in photosynthetic and transpiration rate, in water use efficiency, and decrease in membrane permeability	Song et al. 2014
Citron (*Citurs limon* (L.) Osbek)	45 °C	Reduction in photosynthetic rate, CO_2 assimilation. Alterations in chloroplast, matrix zone expanding and loosing of lamella structure	Chen et al. 2014
Pea (*Pisum sativum* L.)	50 °C	More than 30% reduction in malate inhibited PEPC activity	Chinthapalli et al. 2003
Maize (*Zea mays* L.)	45 °C	Complete inactivation of Rubisco and substantial reduction in photosynthesis and malate-inhibited PEPC activity	Crafts and Salvucci 2002
Wheat (*Triticum aestivum* L.)	45 °C	Suppressed synthesis of some proteins, loss of the normal thylakoid structure, extremely convoluted membranes.	Satpathy and Mohanty 2000
Cotton (*Gossypium hirsutum* L.)	40 °C	Reduced activation of Rubisco	Feller et al. 1998

Table 3

Temperature	Crop	Effects	Reference
42 °C	Mung bean (*Vigna radiata* L.)	Increase in ROS lipid peroxidation, H_2O_2 and proline content; reduction in chlorophyll and relative water content	Nahar et al. 2015
40 °C	Maize (*Z. mays* L.)	Reduction in biomass of maize plant, decrease in concentration of chlorophyll a, b and carotenoids, decrease in RWC	Zhu et al. 2011
40 °C	Potato (*Solanum tuberosum* L.)	Reduction in photosynthetic rate, chlorophyll and carotenoid content, decrease in stomatal conductance	Aien et al. 2011
45 °C	Wheat (*Triticum aestivum* L.)	Reduction in chlorophyll and photosynthetic pigment content, decrease in protein synthesis	Efeoglu and Serpil 2009
33 °C	Rice (*Oryza sativa* L.)	Reduction in chlorophyll content, PS-II activity, and in grain content of starch and its amylose component	Zhong-Hua et al. 2009
40 °C	Sugarcane (*Saccharum officinarum* L.)	Reduction in leaf water potential, relative growth rate, increase in the level of anthocyanins and soluble phenolics, production of ROS lipid peroxidation and damage of chloroplast membranes	Wahid and Close 2007
38 °C	Pea (*Pisum sativum* L.)	Reduction in chlorophyll a, b and total carotenoid contents, Increase in chlorophyll florescence ratio, reduction in chlorophyll a, b protein pigments	Georgieva and Lichtenthale 2006
45 °C	Tomato (*Lycopersicon esculentum* L.)	Reduction in CO_2 assimilation rate, reduction in chlorophyll to carotenoid ratio	Camejo et al. 2005
40 °C	Cotton	Restriction in photosynthesis, enhancement of photorespiration affecting	Wise et al. 2004

| | (*Gossypium barbadense* L.) | the photosynthetic apparatus, and reduction in mesophyll conductance | |
| 50 °C | Maize (*Z. mays* L.) | Reduction in PS-II activity, photosynthetic rate and chlorophyll contents | Sinsawat et al. 2004 |

Table 4

Trait	Source
Membrane stability	Kumar et al. 2012a
Plant stay-green character	Kumar et al. 2010
Leaf with waxy cuticle	Richards 1996
Improved stomata conductance and photosynthetic rate	Nagarajan et al. 2010
Better filling duration and fruit setting	Fahad et al. 2017
Grain yield	Yang et al. 2002

Tables Titles

Table 1: Projected yield losses in major crops by the end of 21st century, owing to an increase of

1 °C in temperature

Table 2: Effect of heat stress on photosynthetic enzymes and apparatus

Table 3: Effect of heat stress on photosynthetic pigments and plant physiological attributes

Table 4: Traits considered to be important for heat stress tolerance

Figure 1

Occurrence of HS in plants
i) Increase in soil and air temperature
ii) Reduction in soil moisture
iii) Changes in soil physical properties and plant canopy properties
iv) Reduction in photosynthesis

Plant response to HS
i) Loss of turgor
ii) Poor germination and stand establishment
iii) Leaf senescence
iv) Tissue dehydration
v) Increase in pollen sterility
vi) Poor seed setting
vii) Reduction in grain growth

Adaptation to HS
i) Growing HS tolerant cultivars
ii) Changes in sowing time
iii) Proper nutrient and irrigation management
iv) Seed priming and spray of osmo-protectants
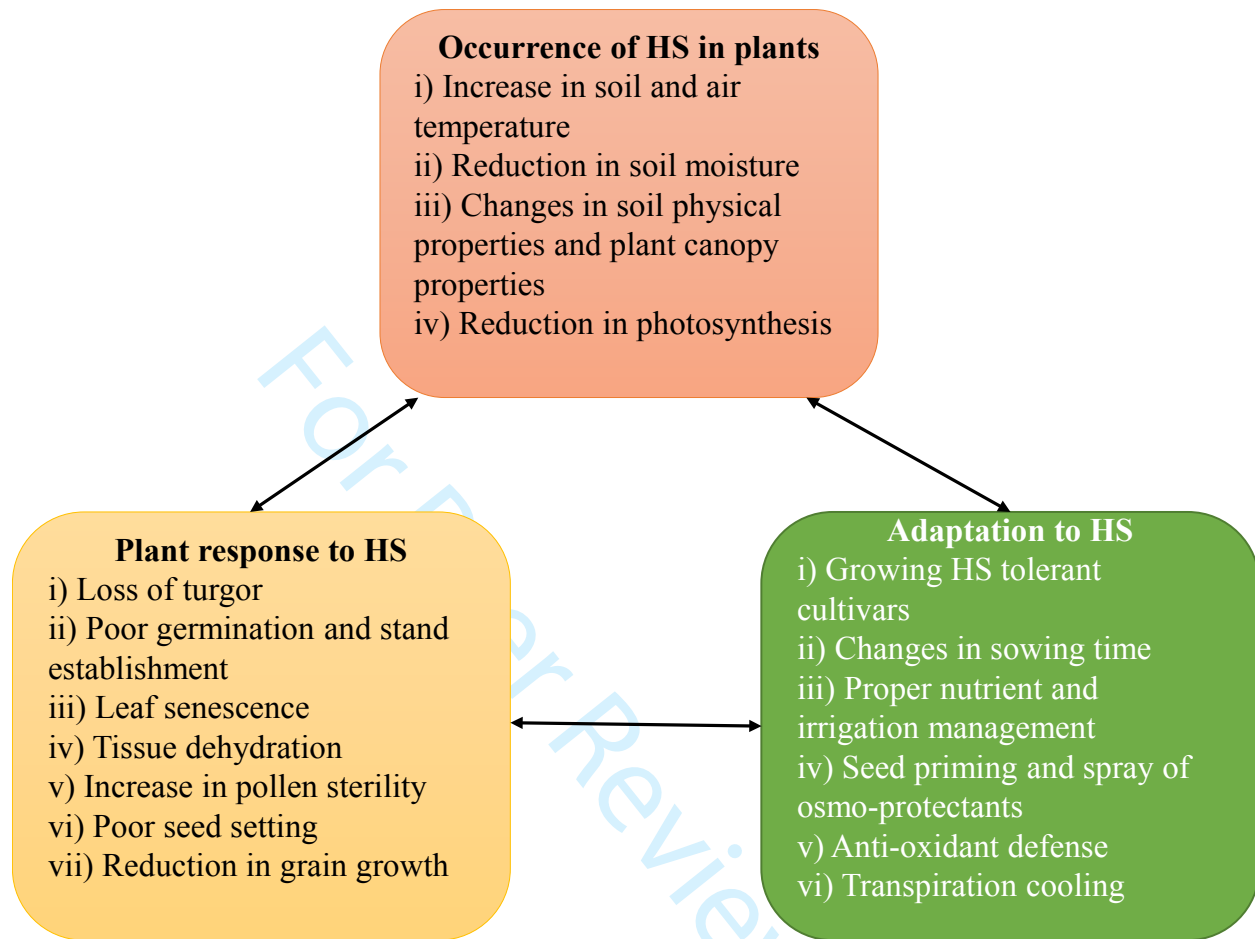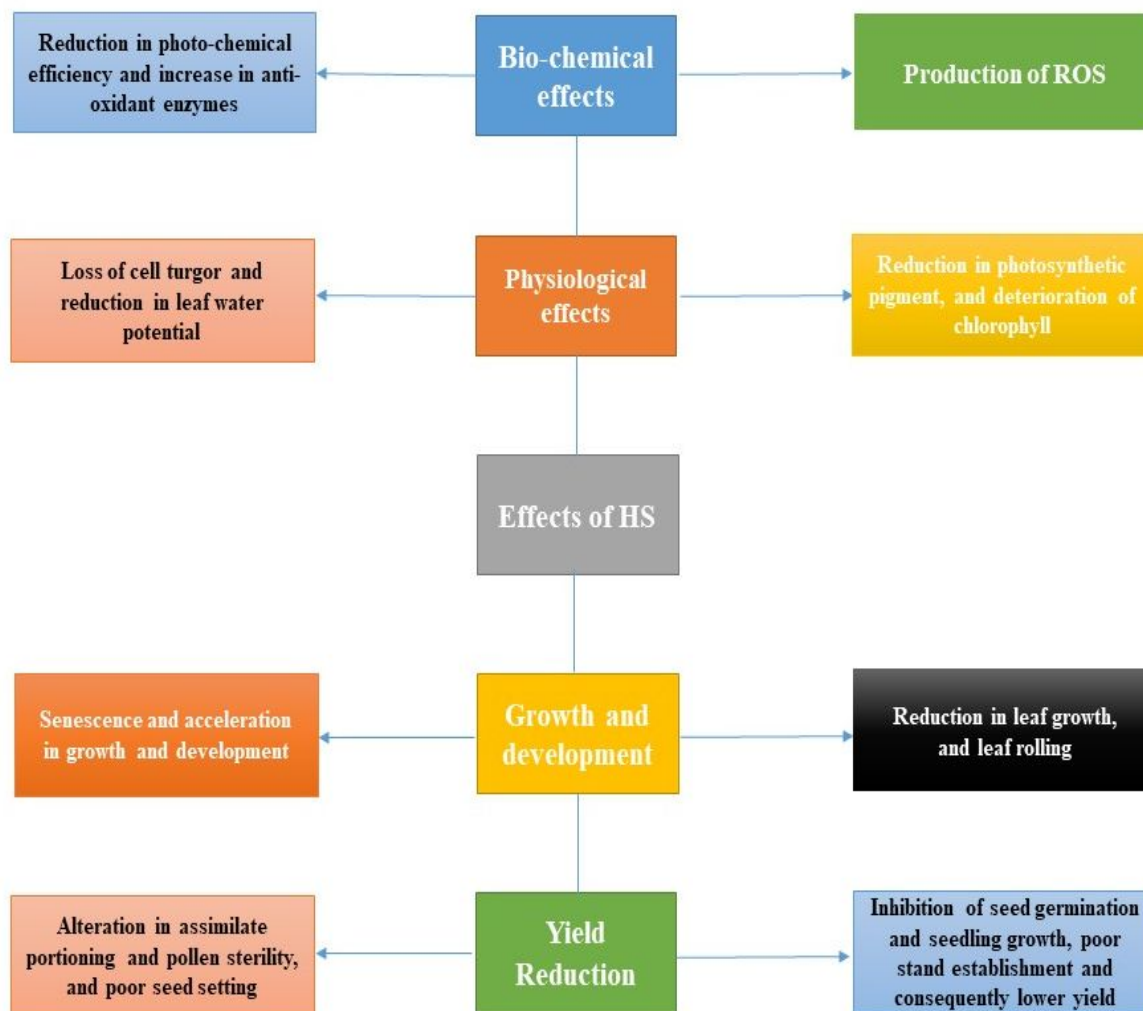v) Anti-oxidant defense
vi) Transpiration cooling

Figure 2

Figure 3

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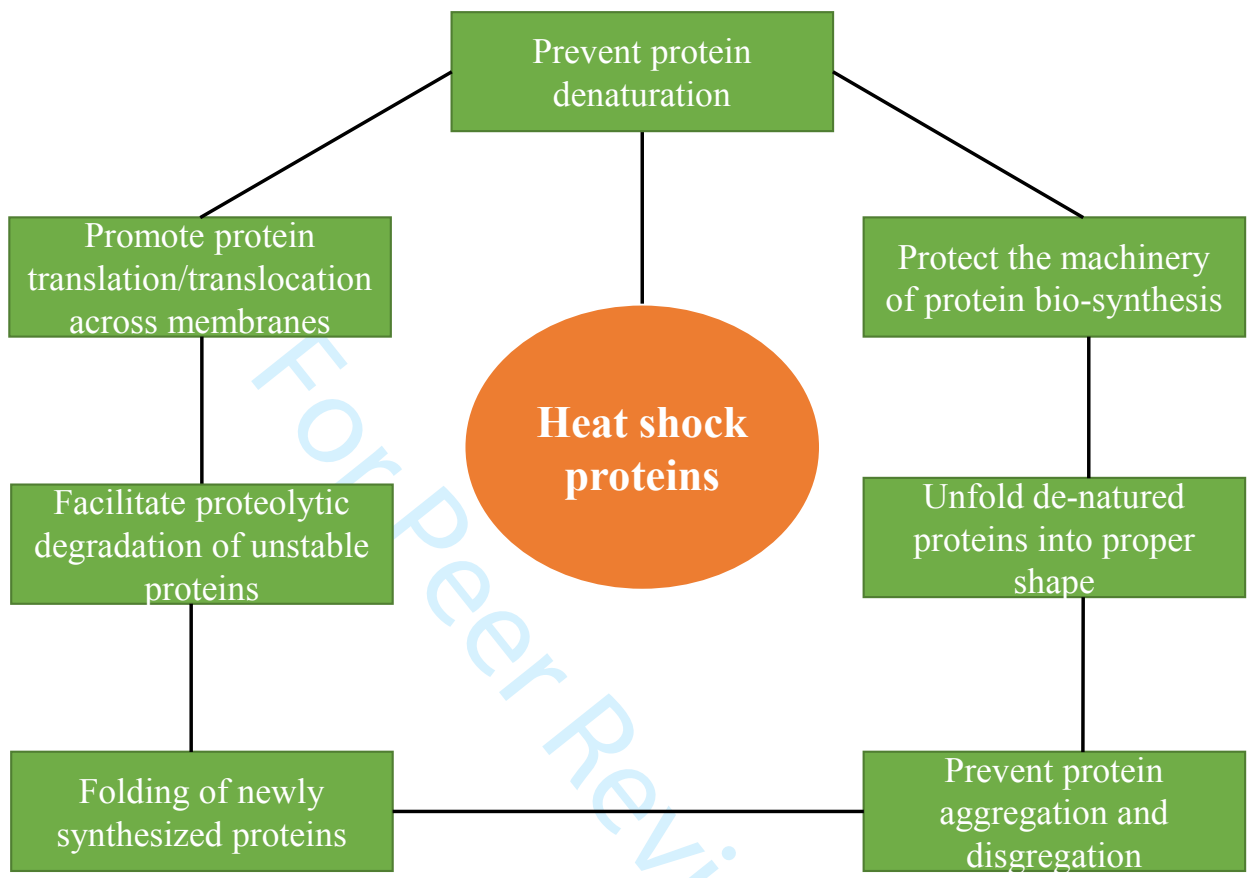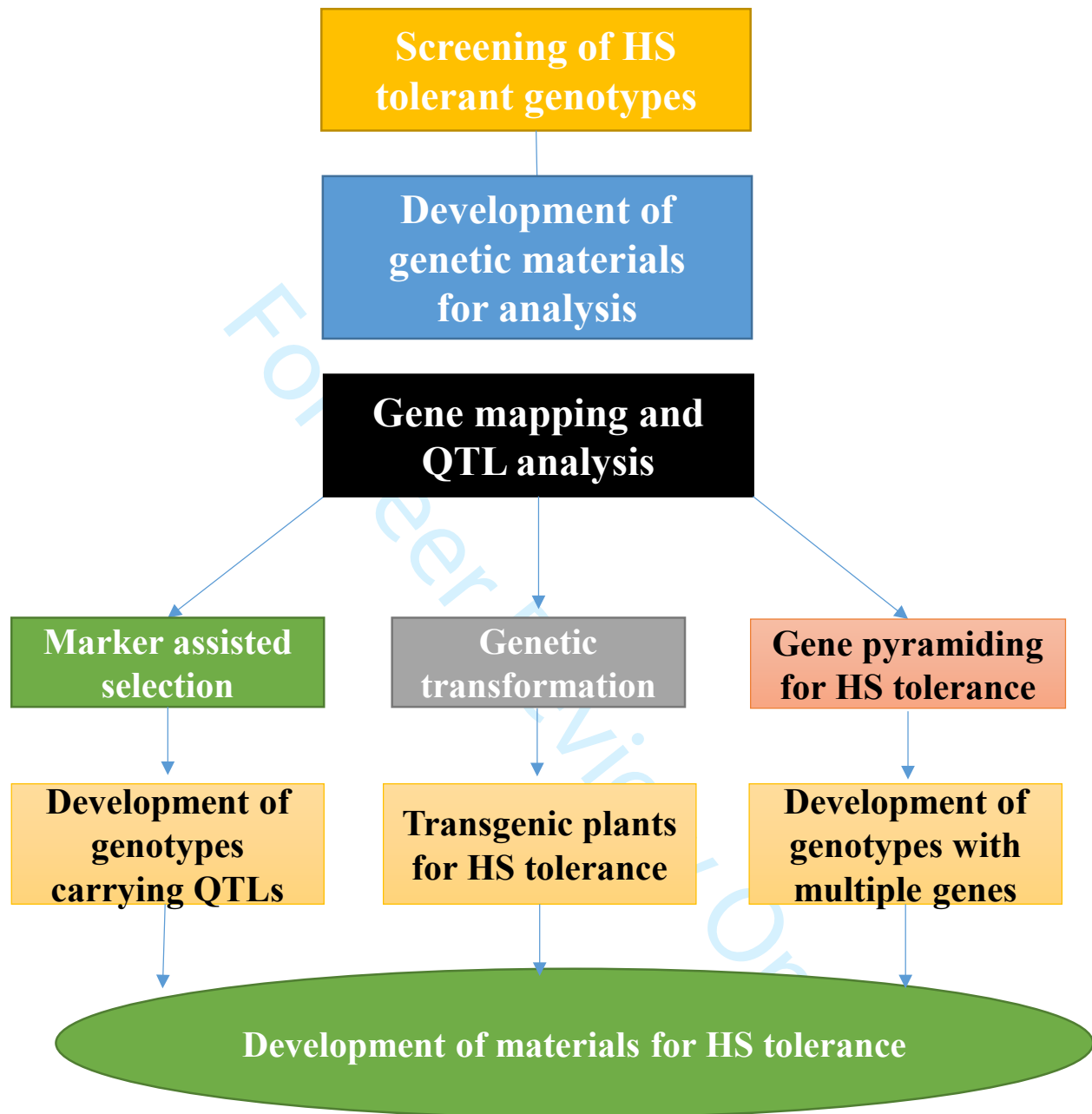51
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Figure 4

Figures Caption

Fig. 1: Main effects of heat stress (HS) on plant growth, physiological and bio-chemical processes, and yield related factors.

Fig. 2: Effects of heat stress (HS) occurrence in farm fields, and adaptation mechanisms.

Fig. 3: Mechanisms of heat stress (HS) tolerance induced by heat stress proteins (HSPs) in plants. HSPs prevent protein denaturation under HS, and protect the machinery of protein synthesis. HSPs also favour protein transport across the membranes and organelles, and facilitate the proteolytic degradation of unstable proteins. Moreover, HSPs unfold the denatured proteins, fold the newly synthesized proteins into proper shape, aggregation and disaggregation under HS, and thus improve plant ability to cope with HS conditions.

Fig. 4: Strategies involved in the development of heat stress (HS) tolerant genotypes, in accordance with the scheme for drought tolerance genotypes (Farooq et al. 2009a). The first step is the identification and selection of HS tolerance in cultivars. Afterwards, the selected genotypes are analyzed for HS tolerance, and genetic material is developed for further analysis. In the next step, gene mapping and QTL analysis are performed. The major identified genes and QTLs are analyzed using a large population, in view of gene cloning. Then, cloned genes bearing HS tolerance are transferred into different genotypes. Marker assisted selection is also used to develop cultivars having genes and QTLs for HS tolerance.