Heat Stress and its Impact on Plant Function: An Update

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Abstract

An astonishing increase in temperature is posing several harmful impacts on crop plants. Heat stress is an abiotic environmental phenomenon that causes limits, inhibits plant growth, metabolism, and productivity worldwide, resulting in losses in production yields. Heat stress is caused by human activities and global warming,s such as greenhouse gases, carbon dioxide, methane, nitrous oxide, and water vapour. There are many pieces of evidence to support that heat stress reduces the crop plants yield worldwide, and the effects of heat stress are challenging to meet nutritional security and global food security for human beings. Heat stress has negative impacts on each developmental stage, including from germination to harvesting. Prevalent approaches for heat adaption is inadequate management that is unable either to increase the crop productivity or sustain ld. Several responses to dissect the relevant knowledge about heat stress mechanism involving morphological phenomena, physiological phenomena, reproductive replies, and molecular responses such as heat shock proteins act as mRNA synthesis, mRNA control (effects of genes during heat stress), the translation process, heat response element. There are such phenomena involving disseminating the knowledge concerning heat stress. In this review, we summarise the effect of heat stress on plant mechanisms, including morphological, biochemical and molecular responses.

Keywords: Heat stress; molecular responses; morphological responses; physiological process;

1. Introduction

Heat stress is a primary concern for agriculture production due to its changes in an irreversible way for crop plants (Hall, 2000). There are many causes for the increase in heat stress, namely greenhouses gaseous, chlorofluorocarbon, human activities and CO_2 assimilation. Numerous models have been put forth to predict climate change's impact on crop yields (Zhou *et al*., 2017). Keeping everything constant in the simulation models has been seen by a study that increases in temperature, which reduces the global yield of maize (7.4%), wheat (6.0%), soybean (3.1%) and rice (3.2%) (Zhou *et al*., 2017). Forecasts predict the frequency and duration of extreme heat events to rise by 50 % in 2050 and 90 % by 2100, resulting in significant yield losses (Handmer *et al*., 2012).

Crops adapted to the warmer regions show better tolerance to high temperatures, as evident in cucumber, cowpea, and cotton (Driedonks *et al*., 2016). While in the excellent season, crops such as lentils and wheat show decreased germination at soil temperatures above 24-26^0 C (Hall, 2000). Rising temperature resulting in heat stress is causing an alteration in the mechanism of crop plants, including morphological, physiological and molecular (Porter, 2005). Heat stress leads to the death of cells within minutes or could destroy the whole plant (Schoffl *et al*., 1999). Out of all the factors, the timing and duration of heat stress have the worst effect on plant growth (Dufault *et al*., 2009). Heat stress damage is severe when it coincides with the critical crop development stage, particularly the reproductive stage (Rieu *et al*., 2017). The reproductive stage is highly vulnerable to damage and thus causing significant yield penalties (Telfer *et al*., 2013).

Heat stress is causing direct or indirect effects on plants, including protein, lipid denaturation, mitochondria death, membrane degradation resulting in plant death. Eventually, these direct and indirect effects lead to cells' starvation, ion flux reduction, toxic compounds production, etc. (Howarth, 2005). Heat stress ultimately results in molecular, transcriptional, phenological and physiological changes for plant growth and survival. Different crops plants can tolerate a specific threshold temperature without significant damage to their development and mechanism. This review summarizes the effect of heat stress on plants mechanisms and different changes induced in the plants.

2. Responses of plants during heat stress:

Heat stress is a significant problem for plants that limits and restricts plants' growth, development, metabolism, and productivity. Therefore, alternation of these responses may positively and negatively impact both (Figure 1). These effects may be on plants, including morphological, physiological, hormonal response and biochemical responses.

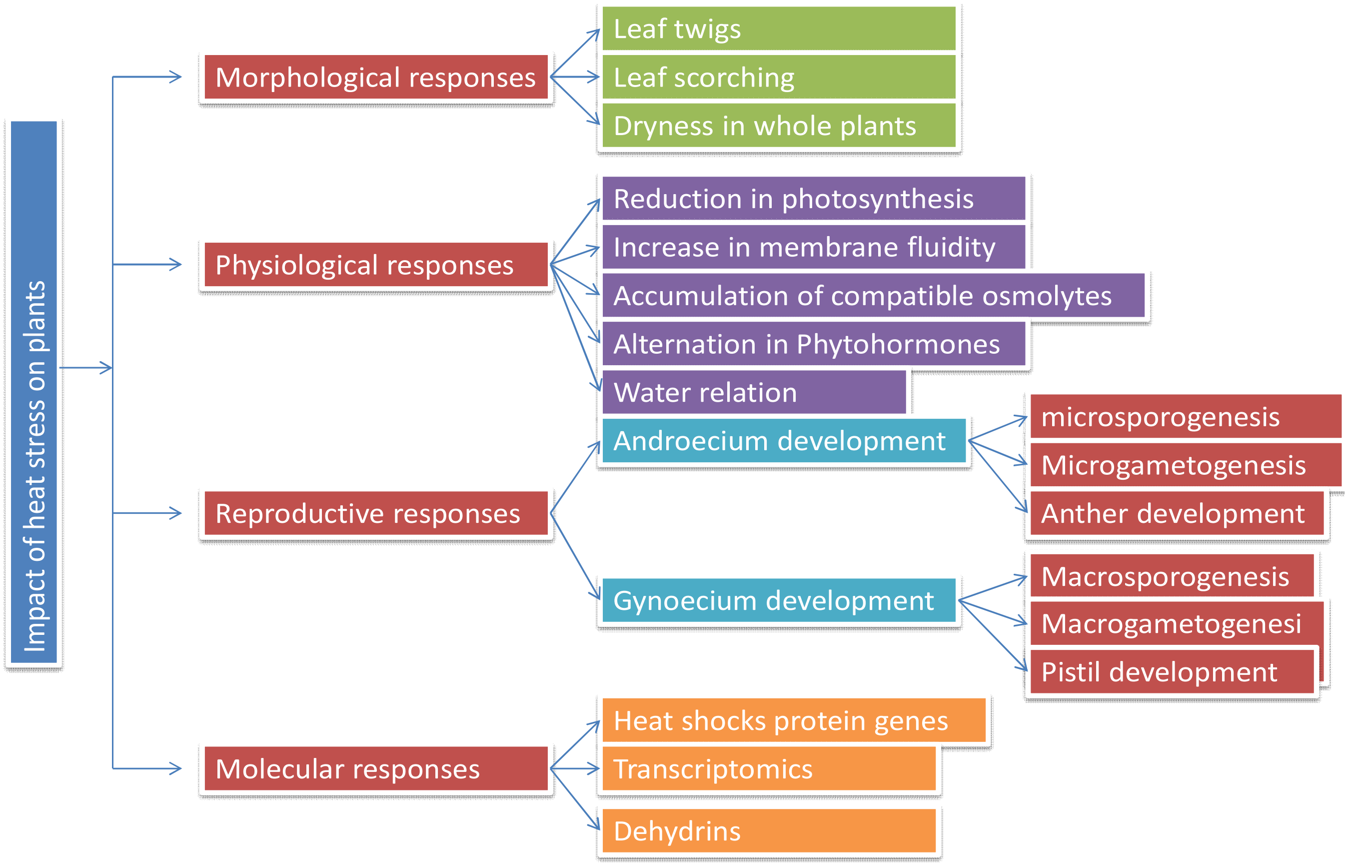

Figure 1. Schematic representation impact of heat stress on plants developmental stage.

2.1. Morphologiccal responses

In a tropical climate, heat stress is the limiting factor affecting crops growth, plant development stage, and crop yield. Heat stress causes significant limitations in all crops, including wheat, rice, maize, pearl millet, sorghum, barley, brachypodium, arabidopsis, pea and tomato. Heat stress has an irreversible effect on pre and post-harvest losses, including sunburn on leaves, scorching and twigs on leaves, stem, shoot, root growth inhibition, fruit discolouration, and reduced yield (Vollenweider and Günthardt-Goerg, 2005). In addition, heat stress reduces the total biomass, indirectly influencing the characters associated with biomass production. However, morphological appearance can be seen in every plant stage involving the physiological and reproductive stages. For instance, heat stress would reduce seed germination capacity, loss of vigour, reduce seedlings, and ultimately destroy the plants. These responses may differ from the phonological stage to other stages. Another example, heat stress reduced coleoptile at 40^0C and ceased at 45^0C in maize (Weaich *et al*., 1996).

Moreover, it has been seen that one of the effects on shoot growth of plants is effected in which the first internode of shoot growth and some other internodes is inhibited by heat stress. For instance, sugarcane exhibited smaller internodes, high tillering capacity, and ultimately reduced total biomass production (Ashraf and Hafeez, 2004; Wahid *et al*., 2007; Sharma *et al*., 2017). Some other example, in wheat, the optimum temperature 12^0C to 22^0c is required for anthesis and grain filling, respectively; both grain number and grain size must have been affected by heat stress besides the number of grains per ear at maturity is declined with increase heat stress (Tewolde *et al*., 2006).

2.2. Physiological activity under heat stress

Heat stress causes irreversible changes in the physiological activity of plants resulting in losses in crop plants yields. Several ways are to reduce the dangerous effect of heat stress by developing the new cultivar. Physiological activity exhibiting one of the best measurements under heat stress, including stomata closure, cell membrane thermostability, canopy temperature, chlorophyll content. Stomata conductance is a good indicator because it reduces transpiration and photosynthesis activity (Crafts-Brandner *et al*., 1997; Morales *et al*., 2003). One way to reduce the heat stress is by evaporation from leaves when stomata are opened that cool the plants. Stomata conductivity during the day is enhanced by evaporation, which cools plants' surrounding environment; this phenomena reduce the temperature around the plants. However, stomatal conductance is inhibited by the heat temperatures due to a decrease in the rubisco protein (Crafts-Brandner *et al*., 1997; Morales *et al*., 2003). Stomata must be helping to eliminate the heat stress because it involves regulating the transpiration rate and determine the degree of cooling of plant leaves. Moreover, the broader opening of stomata rate must increase transpiration and photosynthetic activity; this is occurred by the diffusion of water vapours and CO_2 through the stomata. Numerous studies show that stomatal conductance and photosynthetic activity support detecting heat stress (Azhar *et al*., 2020).

In 1974, Sullivan suggested the protocol of cell membrane thermostability (Sullivan, 1972). Moreover, cell thermostability is controlled by a small number of genes and used to detect crop plant heat stress genotypes for example in soybean (Martineau *et al*., 1979), potato (Coria *et al*., 1998), Sorghum (Marcum, 1998), Barley (Wahid and Shabbir, 2005), tomato (Golam *et al*., 2012), Rice (Maavimani *et al*., 2016). In addition, cell membrane thermostability is a good indicator in which electrolytic leakage from leaf disks are exposed during heat stress. Moreover, chlorophyll fluorescence and membrane leakage is a sensitive method for quantifying the responses of cotton during high temperatures. Hence cell thermostability is a good measure for heat stress.

In addition, canopy temperature measures the heat stress in plants. Canopy temperature is calculated using the physiological inframeter technique in which several genotypes are detected (Singh *et al*., 2007). In addition, photosynthesis phenomena are more sensitive and have adverse effects on plants, including C_3 and C_4 plants (Young *et al*., 2004). during heat stress. Photosynthetic rate mainly depends on CO_2 concentration in the leaf intracellular, especially in C_3 plants. When photosynthesis occurred in thylakoid lamella and carbon assimilation in the stroma in the chloroplast, it is the primary site where photosynthesis is reduced (Wise *et al*., 2004). Photosynthetic is affected by the activity of the supply of carbohydrates in the developing walls.

Moreover, photosynthesis and chlorophyll content is decreased during heat stress. In addition, reduction of chlorophyll a :b the ratio was more pronounced than developed leaves under high temperatures (Karim *et al*., 1997). These effects on plants show that chlorophyll and photosynthetic activity is reduced with the production of active oxygen species. Heat stress poses several negative phenomena on plants involving reduced leaf area and water potential that negatively impact photosynthesis of plants. In which photosynthesis transitions from noncyclic photophosphorylation to cyclic photophosphorylation and changes in photosynthetic activity occur by the destruction of electron transport, several proteins, and damages of photosynthetic pigment. In the vegetative stage, high temperature decrease the physiological mechanism in the leaf in that CO_2 damage the component of photosynthesis II in thylakoid membrane of chloroplast and resulted in membrane damage (Hall, 2004). The changing of photosynthesis rate along with transpiration rate is a primary indicator of heat stress. During heat stress, significant alternations in chloroplast, thylakoid stability disturbance, swelling in grana in which carbon metabolism activity in the stroma taking place in thylakoid is a disturbance.

Moreover, heat stress has a negative effect on photoinhibition of photosystem I and photosystem II (Yamori *et al*., 2016; Yamamoto *et al*., 2019; Kono *et al*., 2014). Under moderate heat stress, plants maintain a balance or protect themselves from excess electrons when light fluctuates. In this direction, Tana *et al*. 2019 investigated that PSI photoinhibition in tobacco leaves at either 25^0 Cor 42^0 C is caused by the fluctuating light. PSII transfers an electron to PSI; then PSI is damaged immediately because PSI cannot consume soon by electron sinks. Moreover, photosynthesis is limited by photoinhibition of the two photosystems, i.e., PSI and PSII. These two photosystems, either PSI or PSII, limits the photosynthetic CO2 assimilation. The CO2 oxide assimilation rate per unit area in C_4 plants is higher than that of C_3 plants, and more assimilation power is required (Atkinson *et al*., 2016). Ting *et al.* reported that PSII was significantly inactivated after Heat temperature in maize. Identical results are found in previous research in C_4 plants sweet sorghum (Yan *et al*., 2013).

In addition, respiration is vital for photosynthetic, if respiration is inhibited, then suppression of photosynthesis and aggravates of photoinhibition is occurred (Dinakar*et al*., 2010; Gardeström and Igamberdiev, 2016; Nunes-Nesi *et al*., 2011). Limitation of respiratory electron transfer inhibits photorespiration and hence aggravates photoinhibition (Zhang *et al*., 2017). The efficiency of oxidative phosphorylation is occurred by disturbance of mitochondrial membrane structure. Moreover, the nuclear genome encodes many chloroplast proteins when nuclear envelopes resulting in inhibition of the photoprotection mechanism, hence repair of photoinhibition and structural damage is damaged and delayed by aggravating photosynthetic mechanism (Tana *et al*., 2019).

Moreover, the respiration rate seemingly increases when the temperature is above 40-50^0C. This high-temperature affect and damage to respiratory mechanism. Heat stress involves increases in respiratory carbon losses, reduction in ATP production, and increases in ROS production in which kinetics of rubisco and CO_2 solubility are adversely affected. The rubisco enzymes catalyze photosynthesis and photorespiration, the rate of rubisco enzyme mainly depends on oxygenase and carboxylase enzymes (Laing *et al*., 1974). The mesophyll concentration of CO2 limits carboxylase activity. Photosynthetic activity is reduced by the CO_2 losses that led to photorespiration.

2.3. Hormonal response

Several plants hormones are responsible for maintaining the plants during heat stress. Such plants hormones such as abscisic acid (ABA), salicylic acid (SA) and ethylene are increased, and some hormones such as auxin, cytokinin and gibberellin acid are decreased under heat stress (Larkindale and Huang, 2005). ABA is an abiotic stress hormone that is responsible for combating heat stress. Moreover, it mediates the biosynthetic pathway in which it maintains the heat stress by closure the stomata by osmotic pressure. Furthermore, Abscisic acid save plants under heat stress to alter the expression of several numerous genes. Moreover, it is also related to reactive oxygen species (ROS) generation in guard cells through rubidium hydroxide (Rboh) regulation (Miller *et al*., 2008).

Furthermore, ethylene plays an indispensable role because this is found in gases form that regulates the growth of plant and development of plants by controlling seed germination, fruiting and stress tolerance (Munné-Bosch and Alegre, 2007). The effect of ethylene production during heat stress varies from plant to plant. There are many examples have been proved that either high stress is beneficial for plants or are not, for instance, in soybean, 40^0C temperature increase the production of hypocotyls, but in wheat, 40^0C inhibit the ethylene production in leaves (Tan *et al*., 2011; Wahid *et al*., 2007).

Furthermore, salicyclic acid (SA) is involved in heat shock responses (HSRs) too. SA prevents oxidative damage to membranes through detoxification of superoxide radicals. Salicylic acid provides strong thermotolerance in plants by association with heat shocks protein (HSP) genes, antioxidant phenomena that improved fertility and increased yield (Larkindale and Knight, 2008). Some other hormones just opposite to ABA, such as gibberellins and cytokinins are involved with heat tolerance. The concentration of these hormones is being declined by roots and shoots growth and dry accumulation under heat stress. In addition, it has been proved that the amount of endogenous auxin is reduced under high temperatures, mainly in anthers (Teale *et al*., 2006).

2.4. Reproductive response

As we know, plants can give high performance in a suitable condition, but under heat stress, the plants survival rate is meager; if they do not change the abnormal environment, they cannot survive hopefully in that environment. Therefore, plants alter the mechanism activity to increase the frequency of survival rate under heat stress conditions and give the expected yield. During the reproductive stage, there are various activities occurred under heat stress (Table 1). There is many reproductively activity such as inflorescence development, sporogenesis, gametogenesis, anthesis, pollination and fertilization etc. (whole reproductive activity during heat stress).

Table 1. Schematic representation impacts of heat stress on plants reproductive phase with effective temperature for survival to plants

Crop	Growth stage	Control temperature (^{0} C)	Extreme temperature (^{0} C)	Duration of treatment	Plant response studied	References
Rice (*Oryza sativa*)	Inflorescence development	25	37	Continuos	Pollen sterility	Matsui *et al*., 1997 Prasad *et al*., 2006
	Microsporogenesis	28	33	Continuos	Reduced pollen production, Pollen inviability	Endo *et al*., 2009
	Pollen maturation	28	39	2-4 days treatment	Downregulation of expression of tapetum genes	Jagadish *et al*., 2007 Yoshida and Nagato, 2011
	Anthesis	30	>33.7	1hr treatment at anthesis	Pollen sterility	
	Pollination	28	38	4hrs treatment	Spikelet sterility	
Wheat *(Triticum aestivum)*	Inflorescence initiation	25	30	Continuos	Early anthesis	Friend *et al*., 1963 Omidi *et al*., 2014
	Inflorescence development	26	33	Continuos	Meiotic abnormalities Male sterility	
	Microsporogenesis	20	30	3 days treatment		Ferris *et al*., 1998 Wardlaw and Moncur, 1995
	Anthesis	28	38	Whole day at anthesis	Less grains per ear	Gibson and Paulsen, 1999

	Post anthesis	18	30	Continuos	Reduced kernel weight	
	Post fertilization	20	35	15 days after anthesis to maturity	Yield reduction	
Barley *(Hordeum vulgare)*	Inflorescence development	20	30	5 days (after floral initiation	Pollen inviability	Sakata *et al*., 2000
	Microsporogenesis	20	30	5 days after floral initiation	Abnormal microspores	Sakata *et al*., 2000
	Microgametogenesis	20	30	1-5 days (after fifth leaf formation)	Pollen abortion	Abiko *et al*., 2005
	Pollen maturation	20	30	From four leaf stage	Anther wall degradation	Oshino *et al*., 2007
	Post anthesis	20	40	15-20 days after anthesis	Reduced grain weight	Savin *et al*., 1996

Brachypodium (*Brachypodium distachyon*)	Inflorescence initiation	24	32	Continuos after three leaf stage	Less tillering	Harsant *et al*., 2013
	Microgametogenesis	24	36	Continuos after three leaf stage	Less pollen germination	Harsant *et al*., 2013
	Anthesis	24	36	Continuos after three leaf stage	Reduced grain weight	Boden *et al*., 2013
	Pre-fertilization	24	32	Continuos after three leaf stage		
	Pollination	22	27	During flowering		
Maize (*Zea mays)*	Inflorescence development	33.9	>35	14 days (before silking)	Male and female sterility	Cicchino *et al*., 2010
	Anthesis	27	38	2 days (before anthesis)	Reduced pollen germination	Herrero and Johnson, 1980
	Pollination	27	38	2 days (before anthesis)	Poor kernel set	Herrero and Johnson, 1980
	Pre silking	25	35	14 days (before silking)	Decrease in ear weight	Suwa *et al*., 2010
Sorghum (*Sorghum bicolor*)	Inflorescence initiation	25	37	Continues	Floret sterility	Prasad *et al*., 2015 Singh *et al*., 2016
	Inflorescence	30	38	Continues		Downes, 1972

	development Anthesis Post anthesis	28 32	33 40	Continues Continues	Reduced pollen germination Embryo abortion Lesser grain yield	Prasad *et al*., 2006
Pearl millet *(Pennisetum glacum)*	Inflorescence Development	35	>42	Continues	Reduced seed set	Jukanti *et al*., 2017
Arabidopsis (*Arabidopsis thaliana*)	Inflorescence development	22	42	4hrs treatment	Pollen release is impaired	Kim *et al*., 2007
Pea (*Pisum sativum)*	Inflorescence development Inflorescence development Anthesis Post fertilization	20 20 20 24	33 30 28 32	6hrs treatment 6hrs treatment 6hrs treatment for 2-4 days 6hrs treatment	Abortion of floral buds Less flowering nodes Lesser number of seeds per pod Reduction in yield	Guilioni *et al*., 1997 Guilioni *et al*., 2003 Guilioni *et al*., 2003 Guilioni *et al*., 2003
Tomato (*Solanum lycopersicum*)	Inflorescence initiation Inflorescence development Microsporogenesis	28 18 28 28	>29 28 32 35	Continues Continues 15 days(before anthesis) Continues	Reduction in fruit yield Reduce Stigma Surface Area Reduced expression of Proline Transporter I Stigma exertion without anthesis	Peet *et al*., 1997 Sawhney and Polowick, 1985 Sato *et al*., 2006 Lohar and Peat, 1997 Peet *et al*., 1997

	Microgametogenesis Pollen maturation	25	29	From flower initiation to maturity	Decrease fruit set Inviable pollen	Pressman *et al*., 2002
	Anthesis	28	32			

2.4.1. Inflorescence development

As a next developmental step, floral organs originate in the spikelets formed on the central axis of inflorescence or its branches. In 1991, the research found that the ABC flower development model is found on the floral homeotic mutants in *Arabidopsis thaliana* and *Antirrhinum* (Coen and Meyerowitz, 1991). The original model proposed three significant classes of *MINICHROMOSOME MAINENANCE FACTOR AGAMOUS DEFICIENS SEPALLATA GENE* (MADS-box genes). Combined expression of these specific genes leads to the formation of the four successive whorls thus specifying the floral organ identity. Progressing inwards, outermost whorl contains sepals, a second whorl consists of petals, a third whorl consists of stamens, and finally a fourth whorl is composed of carpels.

Over the past three decades, this model has grown more complex and D class genes were introduced that regulate ovule identity and development within the carpel (Angenent *et al*., 1995; Colombo *et al*., 1995). Finally, this model was enhanced by the addition of four other MADS genes (SEPALLATAs: SEP1, SEP2, SEP3, and SEP4) that define the floral nature of flower organs along with A, B, C, and D genes in Arabidopsis (Pelaz *et al*., 2000; Theissen, 2001; Ditta *et al*., 2004).

On the other hand, unlike flowers in Arabidopsis, the monocot flowers are notably different, specifically the external organs. Comprised of glumes and florets, spikelet forms the primary inflorescence of monocot inflorescence. The identity of these organs as sepal equivalents or lemma as bract and palea as prophyll equivalents is highly debatable (Arber, 1934, Kellogg, 2001). However, the most widely used interpretation is the latter one.

Heat stress has a negative impact during a flowering, resulting reduction in floral inflorescence. The main cause of inflorescence reduction is an imbalance in MADS related genes necessary to develop for complete flowers such as floret, sepals, carpels, stamens, petals and whole spikelets. The imbalance in the A gene result not the development of sepals that is necessary for the development of Sepals, moreover combined activity of A and B genes develop the petals, petals may be suppressed in an imbalance of A and B genes under heat stress (Pelaz *et al*., 2000; Theissen, 2001; Ditta *et al*., 2004). Stamens may not be fully developed, and activity of C class genes for development of pistil, it has been suggested that pistil may be affected by the heat stress (Theissen, 2001; Ditta *et al*., 2004).

Exhibiting heat stress than the normal temperature caused earlier floral initiation. This result is exhibited from the flower inducing substances and to be increased sensitivity of meristem cells. It seems that the earlier flower initiation is resulted from the phytochrome balance. Heat stress increases the rate of 730-µm form of the pigment of 660 µm in absorbing structure. In long-day plants, this temperature retardant the flowering and indicates that 730 µm stimulating the flowering (Hendricics, 1960). However, Exposure of high temperature during the day (36^{0}C) at low temperature during (26^{0}C) night for 5 day causes heat stress and reduces the floral fertility than that of optimum temperatures (31^{0}C). It is compared that 10, 5 and 0 days before anthesis reduced the floral fertility in sorghum. If temperature occurred 15 days before than it ultimately reduces the floral fertility. The most sensitive period for floral is 10 days to 5 days before anthesis.

2.4.2. Microsporogenesis/megasporogenesis:

Meiosis is occurred in both pollen and megaspore mother cells of the anther and ovule, respectively, that have differentiated from sporogenous cells through several rounds of mitotic divisions (rice, wheat, barley, Brachypodium, maize, sorghum, pearl millet, arabidopsis, pea and tomato) (Bhatt *et al*., 2001). Furthermore, *EXCESS MICROSPOROCYTES1 OR EXTRA SPOROGENOUS CELLS* (*EMS1/EXS)* define a signalling pathway for tapetum differentiation. PMCs are formed with no tapetal cells in the absence of these genes, thus resulting into non-viable pollen (Canales *et al*., 2002). The *EMS1/EXS* also express in gynoecium, however, their role in determining ovule identity has not been established yet.

The process of microsporogenesis may be affected by heat stress in that plants develop many irregularities during the developmental process. MADS related transcription factor change own activity under heat stress in which regulation of differentiation process in anther primordium can be changed and have a detrimental consequence on the progress of pollen mother cells (Theissen, 2001). On the other hand, the *ameotic1* gene that regulates the switch between meiotic and mitosis in maize and rice is affected by heat stress. In mitotic progression controls the synapsis and recombination, under heat stress, synapsis is converted into asynapsis, and desynapsis and completely suppressed the following process. Many other phenomena reduce or suppress the microsporogenesis and megasporogenesis under heat stress. However, the role of protein kinase for initiating the meiotic process is completely affected by heat stress. Protein kinase changed the way to the regulation of the complete process. Even though the role of protein kinase is less understand under heat stress.

2.4.3. Microgametogenesis/megagametogenesis:

In addition to the structural parameters, several recent pioneering studies utilizing transcriptomic and mutation analyses have instituted the role of crucial genes likely to be involved in germline development and pollen regulatory networks (Borg *et al*., 2009). In >70% of the flowering plants, the embryo sac or female gametophyte exhibit a distinct developmental pattern of polygonum type whereby seven cells of four different types are formed (Maheshwari, 1950). In the developing ovule, the only functional megaspore at the chalazal or proximal end enlarges and undergoes two successive rounds of mitosis without cytokinesis to yield a four-nucleate structure, with two nuclei at each pole. Furthermore, a third mitotic division followed by phragmoplast and cell plate formation between sister and non-sister nuclei marks the beginning of the cellularization process wherein the gametophytic cells are surrounded by cell wall (Maheshwari, 1950; Schneitz, 1995).

It is reported that the reproductive organ is less sensitive than that of the male reproductive organ. However, it is reported in many studies that female reproductive is sensitive with heat stress and differentiate across different crops. Heat stress has an adverse impact on eggs, syndergids, embryo sac, decreases ovule, and some other abnormalities on the ovule. In which, decrease the female gametophyte expansion, and division of the egg and synergids cells is occurred (Saini *et al*., 1984). Moreover, heat stress decreases the adenosine triphosphate concentration and total soluble carbohydrates in the pistil and causes irreversible pre-pollination changes on pistil and post-pollination.

On the other hand, in pearl millet, the female reproductive tissue is more sensitive than the male gametophyte. More significant oxidative damage in pistils than the male pollen grains under heat stress; this result is shows by the activity of antioxidant enzymes and accumulation of ROS (Gupta *et al*., 2015).

2.4.4. Anthesis

Anther dehiscence in both self and cross-pollinated species should be carefully regulated for successful development and timely disposal of the pollen. For this timely process, the pollen grains must be released from the locules of the anther via degeneration of the specific cell types, specifically septum and stomium in the anther cell wall (Scott *et al*., 2004). It has been suggested that mature anther loses water either through transpiration or via active resorption through the filament regulated by *SUC1*, a plasma membrane H^+-sucrose symporter causing an accumulation of sucrose resulting in increased water uptake (Stadler *et al*., 1999). Likewise, various cellular and metabolic changes occur during these steps, as evident from several recent genetic studies in Arabidopsis and rice (Ranjan *et al*., 2017). However, the developmental switch that triggers the flower to enter anthesis still needs to be discerned.

2.4.5. Fertilization

The fertilization process may be disturbed by the heat stress, irreversible changes on fertilization including disrupted structural interaction between anther and stigma either maturation of anther or stigma is on another time (Saini *et al*., 1984). And, reduction of carbohydrates on pollen reduces the adhesion during heat stress and reduces the energy and pollen grains that do not reach stigma. On the other hand, several studies show that the distribution of pollen grains under heat stress may alter the function of cytoskeletal structure, resulting in changes in isoform content of tubulin that disturb accumulation and secretion of vesicles which have a directly adverse effect on cell wall.

An increasing level of auxin during fertilization play indispensable role for germination of pollen and elongation of pollen on the pistil. For example, in rice, auxin plays an important role in pollen tube elongation on the pistil. Under heat stress, the ratio of auxin decrease in pistil, resulting in spikelet sterility (Zhang *et al*., 2018). Another study shows that ROS levels in pistils and a relationship between ROS and auxin levels on pollen may be disturbed under heat stress. In addition, in rice has been reported that the flavonols maintain integrity with the help of regulating ROS homeostasis of pollen tube growth. Flavonols play a vital role in pollen function, tobacco, tomato, maize, petunia the lackness of enzymeflavonol produce an adverse effect on pollen grains (Muhlemann *et al*., 2018).

2.5. Molecular responses

Plants may adopt the condition of heat stress through the molecular responses. Plants exhibit various molecular reactions in which transcriptional units play indispensible role in standing crop plants under high stress. Several genes regulate the transcription process has been proved that these genes regulate some specific activators under heat stress. There are many genes, and their proteins show the expression of under heat stress is briefly described here.

2.5.1. Heat shock proteins:

Several studies have rationalized that genes during heat stress regulate the transcriptional factor within plants because plants signal itself for survival. One of the specific activities is a synthesis of heat shock proteins under heat stress. Heat shock proteins are able to cope with heat stress. There are briefly describing the mechanism of heat shocks proteins (HSPs). HSP may be produced at every stage of plants gradually or successively/ sharply. In all plants majority of HSPs are homologous, which have expression are same in every plants. In which genes alter the mechanism itself by changing the synthesis of mRNA, mRNA stability, translation efficiency, and alternation in protein activity, increasing heat stress (Sullivan and Green, 1993).

It has been proved by studied that promoter region of heat shock proteins genes have heat shock elements in which heat shock transcription factor binds to pentameric nucleotides (5’ -3’) of heat shock elements (HSE) sequence (Perisic *et al*., 1989; Sung *et al*., 2003). These HSE and HSPs interaction and transcriptional activation is conserved. HSPs have occurred very fast, and it varies crop to crop—this phenomenon modified to transcriptional factor expression by a series of genes.

On the other hand, the main function of heat shock proteins is reducing to refolding or deformed (denatured) proteins. HSPs genes have complexity; the main reason behind complexity is found that some compounds in heat shock proteins which is necessary for maturation and development. For example, in rice, starch metabolism and storage protein synthesis elevated the high temperature during the grain filling stage (Yamakawa *et al*., 2007). *Arabidopsis thaliana* shows that heat shock responses network, which has 21 transcription factors that regulate the heat shocks proteins and some other genes, is responsible for regulating transcription activity (Swindell *et al*., 2007). Even though reactive oxygen supplies produce a priceless reaction under heat stress. Hence, the ROS activates the heat shocks factor and confirms that heat shocks genes under heat stress.

Among plants species the proportion of heat shocks proteins may significantly differ. However, three types of proteins are identified in plants based on molecular weight, such as HSP 70 and HSP 90 and lower molecular weight proteins with 15-30 kDa. For example HSP 70 and HSP 90 are expected to increase 10 folds under heat stress, while on the other hand, the lower molecular weight increased by 200 folds. It has been identified that HSP is associated with specific cells structures ex: chloroplasts, mitochondria, ribosomes and cell walls (Schoffl *et al*., 1999; Young *et al*., 2004), for example, maize, rye and wheat seedlings at temperature 42^{0}C in which five molecular mitochondrial proteins weights (19, 20, 22, 23 and 28 kDa) expressed in maize and only one has been expressed in wheat and rye, these proteins have high tolerance in maize compared to another one (Moriarty *et al*., 2002). In addition, HSP68 act as a precursor protein only in mitochondria, but its synthesis increased in cell at high temperatures (Neumann *et al*., 1993).

Moreover, during heat stress, the expression of heat shocks proteins protects the machinery of proteins biosynthesis. Proteins denature under heat stress is prevent by the heat shock proteins. This is believed that the aggregation of small heat shocks proteins plays pivotal role for plants. However, some other proteins are identified, such as HSP 68 and HSP 101. HSP68 is present in mitochondria and has a low molecular weight which is reported in soybean, maize and tomato crops (Neumann *et al*., 1993). In another hand, HSP 101 proteins have excellent characteristics and play role for the renaturation of proteins. HSP 101 proteins are varying crop to crop and also to vary crop stage, for example maize have more expression in tassel, ears, embryo and endosperm compared to that of root and leaves (Young *et al*., 2004). In Arabidopsis, studies show that hot1 and hot 4 genes improve heat tolerance; hot1 is identified as *hsp101* in *Arabidopsis thaliana* (Hong *et al*., 2000). There are many examples related to heat shock protein such as the interaction of HSP 22 kDa with the *Chenopodium album* and Common bean chloroplast membrane effect to the composition of membrane that decreases the fluidity and increased the efficiency of ATP transportation (Barua *et al*., 2003; Simões-Araújo *et al*., 2003). In pumpkin, mitochondrial HSPs proteins have been isolated under high temperatures (Tsugeki *et al*., 1992; Kuzmin *et al*., 2004).

Moreover, some other HSPs are accumulated in the cytosol at 27^{0}C, and in chloroplast at 43^{0}C has been proved that these proteins are produced during photosynthesis. EF-TU 45-46 kDa confirmed that chloroplast stroma protects maize during heat stress (Ristic and Cass, 1992; Momcilovic and Ristic, 2007). The rapid accumulation of HSPs conserves the safety of metabolic apparatus cells. Plants accelerated the significant amount of HSPs to combat with high leaf temperatures in semi-arid andarid areas. In soybean seedling, HSPs regulate the confirmation of some other proteins (Jinn *et al*., 1997). The variant form of HSPs is play a pivotal role to altering the plant responses. Both HSPs64 kDa and HSPs72 kDa are induced under heat stress (Frova *et al*., 1989). A recent study, HSP70 enhanced the heat tolerance in young pea seedlings (Tian *et al*., 2009).

2.5.2. Dehydrins

The term dehydrins are similar with LEA D-11 family. The first case of LEA has been observed in cotton cotyledon in that shifting of mRNA and protein diversity in 18 different distinct family proteins (Hughes and Galau, 1989). In addition, late embryogenesis abundant (LEA) proteins are having a large diverse gene family group involving dehydrins (DHNs). DNHs are produced by latter stage of development of seed under heat stress (Close, 1996). These genes such as cotton to D-11 (Baker *et al*., 1988), rice to RAB 16 which is responsible for ABA (Mundy and Chua, 1984), maize to RAB 17 (Vilardell *et al*., 1990), are cloned and act as DHNs genes in these crops. Several evidence supports the expression of DHNs in cyanobacteria, brown algae, ferns and conifers (Close, T.J.; Lammers, 1993; Li *et al*., 1998; Reynolds *et al*., 1993; Jarvis *et al*., 1996).

Moreover, there are another studied proved that DHNs gene is found in nucleus, cytoplasm, mitochondria, chloroplast etc. (Close, 1996; Campbell and Close, 1997; Wahid *et al*., 2007), and it is also associated with cytoplasmic membrane under heat stress (Koag *et al*., 2003). Moreover, another study revealed that mature embryos of maize is having an accumulation of dehydrin (Godoy *et al*., 1994). Recent studies in sugarcane show that three low molecular weight are reported in leaves, and these three molecules are responsible for heat stress (Wahid and close, 2007). In addition, the responses of plants under heat stress for dehydrative stress may be seen in all developmental stage of plants, including alternation on the flowering stage, low tillering capacity, and growth habit.

2.5.3. Transcriptomic and proteomics

Several previous studies focused on transcriptomic responses of plants for stress combination including heat stress, that revealed the idea of common pattern of gene regulation in different species. Showing the important regulation of gene and gene family for abiotic stress mainly for heat stress which help for developing heat stress crops. Liu *et al*. 2020 reported OsNTL3 is an inducible expression of a processed form that enhances the heat tolerance in rice at the seedling stage. Endoplasmic reticulum regulated the expression of OsNTL3 constitutively. Moreover, soybean plants grow under heat stress and regulate the expression of genes involved in the oxidation-reduction process, protein folding and small metabolic process (Wang *et al*., 2018)

5. Conclusions

Heat stress is more dangerous for crop plants because it would be greatly effected to crop plants growth and development resulting in losses in yields. However heat stress probably depends on climatic zones, duration and timing, these factor of heat stress damaging to crop yields. Main causes of heat stress are occurring by different sources such as global warming and human being. However plants can survive to elevate the high temperature by altering the mechanism of itself under heat stress. During heat stress, plant responses have been studied in developmental stage, however a complete understanding for heat stress is elusive. In recent times, temperatures are being changed season to season and fluctuation of temperature daily has more confusion to define heat stress.

There are many genotypes may tolerate high temperatures. There are many processes in which plants can survive under heat stress such as show the different metabolic pathway and process. Earlier studies emphasise the structure of morphology, physiological activity and molecular structure to understand the mechanism of heat stress. At a physiological stage, plants start the cooling mechanism under heat stress, when temperature is abnormal. Stomata help to leaf cool by transpiration, and, this is reported that stomata is induced during high temperature in the environment resulting to significant reduction in leaf temperature. In addition, understand the activity of specific genes during the developmental of plant is valuable. To tolerate the plants heat stress, at field level, managing the cultural practices, including time of sowing (early and late sowing), methods of sowing and irrigation manner and important selectionof resistance genotypes for heat stress can increase the effects on crops yield. For a response of heat stress, molecular, biochemical and morphological approaches are needed at the field level.

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