Physiological Traits for Improving Heat Stress Tolerance in Plants

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Sourabh Karwa, Akshay Sakhare, Chandrapal Vishwakarma,
Sunder Singh Arya, Madan Pal, and Sudhir Kumar

Abstract

Rice is stable and principle crop that feeds the maximum world population. Under the present climatic change scenario, there is a rise in demand for rice production for sustaining an increasing population as the climatic changes leads to yield reduction and quality deterioration of rice. In rice, anthesis and grain filling are considered as very crucial stages, and any changes in the temperature and water availability cause significant reduction in yield. In this climatic change scenario, the rise in temperature is the most potent factor, which is responsible for the reduction of plant growth and yield. It does not only reduce the yield, but also deteriorates the quality of grains in all agricultural crops. Most of the rice is currently cultivated in regions where temperatures are above the optimal for growth (28/22 °C) if there is an increasing temperature above optimal will result in a reduction in productivity and quality. As the temperature rise caused a reduction in precipitation, this will lead to drought stress. Because of these concerning reasons, the demand for tolerant varieties is increasing nowadays. Physiological and biochemical approaches are proving to be the most important screening tools for the identification/development of tolerant genotypes in any crops under high temperature and drought stresses. The chapter was to focus on identifying the major traits that help in developing the significant adaptive and resilient rice varieties which can sustain high temperature and drought stress. This can act as a potential donor or feeding variety to the current population.

S. Karwa · C. Vishwakarma · S. S. Arya · M. Pal · S. Kumar (✉)
Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi, India

A. Sakhare
Indian Rice Research Institute, Hyderabad, Telangana, India

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4.1 Introduction

The present climatic change scenario is a challenging act in agriculture that causes a catastrophic impact on food security to feed the rapidly increasing world population. The effects of these climatic changes have started showing their impact on the crops' productivity and nutritional quality of all the produce (Kadam et al. 2014). Cereals, mainly rice, wheat, and maize, are essential for present food security demands. In all of these, rice is an important staple crop and a primary source of nutrition to more than 3.7 billion people across the globe (International Rice Research Institute, 2016 http://ricestat.irri.org:8080/wrsv3/entrypoint.htm, accessed on April 10, 2021). Demand for food will increase, as the growing population may be reaching nine billion by 2050 (Godfray et al. 2010), mainly in rice-feeding people living in Africa and Asia (FAO 2014). Even with high production demand, less available freshwater and climate change are posing a severe risk to global rice production (Emerick and Ronald 2019). The projected global temperature will rise by 2.8–4.8 °C by 2100 (IPCC, 2018-19). Repeatedly episode of warmth waves has been reported at the regional scale in the last ten years and had a disastrous impact on agricultural crop production across the globe (Kadam et al. 2014). According to the A1B climate change scenario, approximately 121 million ha of irrigated global rice area is projected to be vulnerable to a high temperature by 2100 (Teixeira et al. 2013). Another critical factor that affects the production was the availability of freshwater crops development and growth. Under these high-temperature scenarios, precipitation levels are also affected, which will ultimately lead to low water. This climate change impacts the earth's crust resulting in infrequent and erratic precipitations, elevated temperatures, and expansion of affected land areas under flood or water deficit. These adverse conditions contribute to the development of the drought-prone regions and, consequently, plant growth and crop productivity.

This stress showed significant detrimental effects on the rice reproductive stage. Rice reproductive stage is considered the most sensitive stage to high stress (HS) (Wassmann et al. 2009; Jagadish et al. 2008; Yoshida 1981). High temperature coinciding at the reproductive stage could result in impaired and poor pollen development, and another dehiscence resulted in high spikelet sterility in rice (Powell et al. 2012; Jagadish et al. 2010a, b). Bahuguna and Krishna (2015) suggested that a high temperature beyond 33 °C (physiological optimum) could affect plant development via alternating molecular and physiological events. Generation of reactive oxygen species (ROS) content is one of the primary events under HS, resulting in the peroxidation of lipids and lower plasma membrane integrity. On the other hand, plants have a robust defense mechanism (antioxidant defense) in maintaining ROS levels under detrimental limits (Szymańska et al. 2017). High-temperature stress also affects the photosynthetic machinery by affecting photochemical reactions in thylakoid lamellae and carbon metabolism within the stroma of chloroplast (Wise et al. 2004; Wahid 2007). Bahuguna and Krishna (2015) suggested that the HS at the later stage could affect the reproductive stage, seed set, and grain filling in rice plants by changing carbon metabolism enzymes and hormonal regulation. Starch synthesis and accumulation during early to mid-grain filling stage result in poor grain filling in HS (Bahuguna et al. 2015).

During flowering, drought stress (DS) on rice has detrimental effects on rice, which resulted in a loss in viability of pollen, pollination failure, and increased flower abortion (Westgate and Ladisch 1993). The key reason for these failures was a reduction in the water potential of floral tissue, i.e., pollen and ovary. Under drought stress, higher production of ROS at the cellular level resulted in significant oxidative damage (Mittler et al. 2004). Short-term and prolonged drought exposure resulted in decreased photosynthesis, leaf development, transpiration, loss of tissue turgor pressure, and various other physiological processes (Tardieu et al. 2018; Jongdee et al. 2002). These changes ultimately affected the anthesis and grain filling stage and resulted in spikelet sterility, and poor grain yield under soil water deficit environment in rice (Jongdee et al. 2002).

Various researchers have studied the impact of these stresses individually, but no reports are available for combined stress effects considered necessary in climatic change. Under natural field conditions, drought and high-temperature stresses can occur concurrently and have more detrimental effects (Rang et al. 2011) than individual stress effects. In Asia, in rice-growing areas, the episode of drought and heat stress at two crucial stages, i.e., flowering and early grain filling, are much every day and responsible for the significant detrimental effect on rice growth and productivity (Wassmann et al. 2009). Other studies documented on various other cereals (rice, maize, wheat, and barley) suggested that combined stress of drought and high temperature showed more detrimental effects than individual ones (Zhang et al. 2013). Heat and drought stresses combined to cause more oxidative stress at the tissue level through overproduction of reactive oxygen species, which damaged protein functions and membrane integrity.

Agricultural crop production faces significant challenges and is considered vulnerable to climatic change like heat spikes, drought spells, increased CO_2, and changing rainfall patterns. Crops productivity was dwindled because of both abiotic and biotic factors. In the above stresses, high temperature and drought are the significant constraints that deteriorated productivity and affect the quality of agricultural food crops worldwide (Schleussner et al. 2018). The rising world population and more demands on agricultural productivity to sustain the world population is a challenging task. Therefore rise in demand for cultivated stress-tolerant crop production to uphold the world population is needed (FAO 2017; Godfray et al. 2010). Crop plants can sense stress responses; adapting and sustaining these responses was carried out by alteration in physiological and metabolisms processes. These advances facilitate us to understate the adaptive strategies of plants in these stress conditions (Bita and Gerats 2013; Basu et al. 2016). Crop productive and metabolite process under these stresses was regulated by using certain growth regulators. Due to these climatic changes variability, plants need to develop adaptive mechanisms, modify their metabolism, or alter specific metabolites to cope with these stresses.

4.2 Rice and Its Importance

Cereals play a significant role in human nourishment, contributing to many calories on a per-day basis. Maize, wheat, and rice contribute 10%, 17%, and 23% calories worldwide (Khush et al. 2001). Among all cereals, rice (*Oryza sativa* L.) is a significant and second most cultivated cereals crop. Rice is grown in flooded conditions and averagely consuming 24.0–30.0% of total available freshwater (Bouman et al. 2007) and requires an optimum air temperature of 32/28 °C day and night temperature. Rice is sensitive to high temperature and drought stress conditions, and the reproductive stage is considered as the most sensitive stage to these stresses (Yoshida 1981; Jagadish et al. 2007, 2008; Sarsu et al. 2018; Basu et al. 2016; Bahuguna et al. 2018). However, the present climate change prediction model suggests a rise of 2.5–4.8 °C temperature by 2100 (Alexander 2016; Masson-Delmotte et al. 2018). As the population demand for freshwater consumption increases and freshwater availability can limit and threaten global rice production (Kadam et al. 2015). In the rice-growing season, the primary concern of drought and HS was conceded at the flowering time, which resulted in S.F. and yield penalty under natural conditions (Matsui and Omasa 2002; Serraj et al. 2011; Liu et al. 2004; Teixeira et al. 2013; Kadam et al. 2015; Pandey and Shukla 2015). Moreover, accurate phenotyping and characterizing a diverse set of germplasms in ambient conditions (field) might give potential tolerant donors which can be utilized in the breeding programs. Although, very few genotypes in rice have been identified and characterized for HS-tolerance.

4.3 Effect of High-Temperature Stress on Rice

Rice's most susceptible stage to high temperature is flowering (anthesis and fertilization) and also some level at micROS porogenesis stage at booting (Yoshida 1981; Prasad et al. 2006; Jagadish et al. 2008; Farrell et al. 2006). The global climatic change in air surface temperature rises significantly by "0.15 ± 0.05 °C" in 10 years (Jones et al. 2016). The present climatic change model predicate that the average rise in air surface temperature will be of "1.4–5.8 °C by 2100" (Corbera et al. 2016).

The optimum temperature that's required for proper rice growth is 32/28 °C day/night temperature. It has been suggested that high temperature at the flowering and grain filling stage was more detrimental in rice (Yang et al. 2007). Peng et al. (2004) revealed the rise in average nighttime temperature by 1.13 °C over 25 years in these stages caused severe damage to growth and yield in rice. It resulted in the sterility of spikelet and decline in yield per plant (Nakagawa et al. 2003). The negative effect of short HS spells has been demonstrated at the flowering stage, resulting in a significantly reduced yield in past decades in China (Welch et al. 2010;

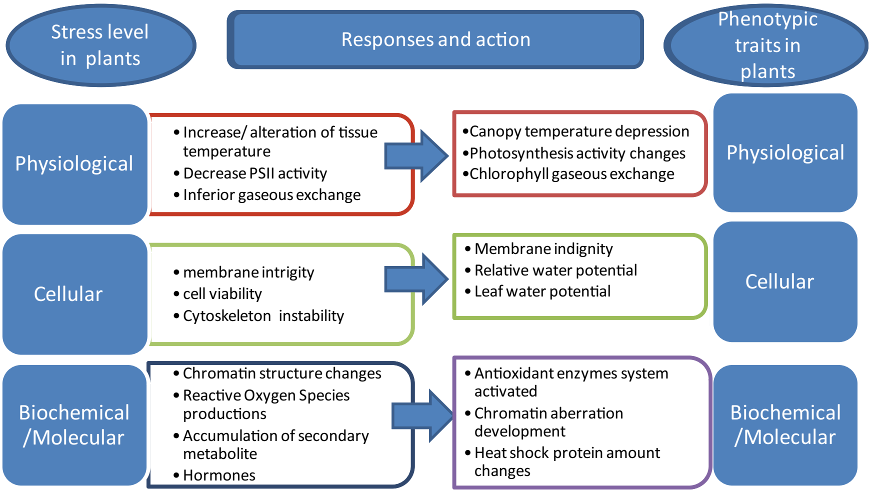

Fig. 4.1 Physiochemical markers to illustrate the effect of high-temperature stress in rice

Yang et al. 2004; Zou et al. 2009). Hasegawa et al. (2009) suggested that high temperatures at the flowering stage result in the reduction of rice productivity. Shi and Chan (2014) investigated popular rice cultivars grown in the high-temperature sensitive region and found much more prone to HS at the flowering stage. For this problem, there is a need to identify true tolerant and high-yielding varieties that did not only sustain but also get yield under HS conditions (Battisti and Naylor 2009; Lobell and Burke 2008). It was reported earlier that N-22 and NL-44 are high-temperature stress tolerance donors at the vegetative and flowering stages by maintaining higher biomass (Bahuguna et al. 2015; Jagadish et al. 2007). Moreover, precise high-temperature phenotyping is needed to characterize germplasms set under natural and field conditions to identify potential donors used in the future breeding program (Fig. 4.1).

4.4 Effect of Drought Stress on Rice

Another major constraint responsible for decreased agricultural productivity is drought or water deficit stress (Sharp et al. 2004; Saini and Westgate 2000). Rice is an irrigated crop and is highly vulnerable to drought (Cabuslay et al. 2002). Around ~23 million ha *Oryza Sativa* L. production is affected by water deficit across the globe (Serraj et al. 2011; Pandey and Shukla 2015). Moreover, its impact is more pronounced because of increased unnatural climatic conditions, which promote drought stress events (Pachauri et al. 2014). As per the climatic model, the frequency of drought spells shortly can be more coinciding with acute stages and results in losses to rice productivity (Kumar et al. 2014). O'toole (1982) reported that drought stress at the vegetative stage result in a lesser reduction in productivity, while the same treatment at meiosis and fertilization results in more considerable yield reduction. At flowering, water deficit resulted in the decline of the grain yield by 30–69% under natural conditions (Cabuslay et al. 2002; Garrity and O'Toole 1994; Sheoran and Saini 1996). Water deficit resulted in stomatal closure and limited carbon accumulation in plants. Leaf water potential was also affected, which diminished turgor pressure in leaf and inhibited stomatal activity and another metabolism (Jaleel et al. 2008). Under drought stress, various plant physiological and biochemical processes were hindered such as membrane integrity, plant water relation, gas exchange, osmolytes content, nutrient management, source-sink association, and growth (Farooq et al. 2008; Benjamin and Nielsen 2006; Jaleel et al. 2008; Razmjoo et al. 2008). Breeding efforts for developing drought resistance rice cultivar that will perform under these predicated climatic change scenarios, but the drought resistance mechanism is poorly understood at the flowering stage (Cabuslay et al. 2002; Condon et al. 2004).

4.5 Effect of High Temperature on Rice Grain Yield, Pollen Viability, and Spikelet Fertility

The flowering stage in rice is most prone to HS and D.S. concerning the vegetative stage (Yoshida 1981). At flowering or anthesis, pollen containing anthers further followed to micro-gametogenesis is the most sensitive tissue to HS and drought stress (Satake and Yoshida 1978; Sheoran and Saini 1996; Nakagawa et al. 2003). The previous report from Yoshida (1981) suggested that manual pollen shaded from non-stress plants to stress stigma showed an ability to fertilize at 41 °C in rice. Therefore pollen grains in the reproductive organ are responsible for lesser S.F. and grain yield in *Oryza Sativa* L. (Wassmann et al. 2009). A study performed in rice at 35 °C for 5 days during panicle development to anthesis suggested a 35% decline of spikelet fertility (Yoshida 1981). A similar response has been conformed in wheat under high temperatures (Saini and Aspinall 1982).

High-temperature tolerance is mainly associated with three primary mechanisms, i.e., avoiding, escaping, and withstand adverse weather conditions. In avoiding high temperature, stress plant adjusts its tissue temperature by maintaining transpiration rate (Weerakoon et al. 2008). Escaping was associated with early morning flowering and avoiding during peak hours (Ishimaru et al. 2010). Another process is to withstand the adverse climatic conditions with resilient developing reproductive physiology (Jagadish et al. 2010a, b). Based on a field study, Prasad et al. (2006) demonstrated that a rise in 5 °C above ambient temperature significantly reduces spikelet fertility, grain yield, and reduction in harvest index, in various rice cultivars was mainly genotype-dependent. They have also shown a strong positive correlation between S.F. and pollen receptivity and pollen production. A similar response is reported in Japanese cultivars by Matsui et al. (2001) and attributed mainly because of the lower pollen count and poor anther dehiscence on the stigma surface. Jagadish et al. (2007) conducted a controlled environment study in rice and reported that at flowering <1 h, high-temperature exposure was sufficient to decline spikelet fertility. It is related to the fertilization and anther dehiscence in a genotypically dependent manner. Other reports suggested that flowering patterns or early flowering attributes under high temperature can be an essential adaptive trait associated with HS (Jones et al. 1997; Ishimaru et al. 2010).

A comparative study by Fu et al. (2008) reported that HS under field and greenhouse recommended that rise in daily mean temperature was responsible for the reduction of spikelet fertility (6–16%) and grain yield and one thousand grain weight in sensitive genotype more as compared to a tolerant hybrid. Jagadish et al. (2008) reported that 6-h exposure to high temperatures at 33.7 °C and 36.2 °C showed a reduction in spikelet fertility and affected the flowering pattern of rice genotypes. Similarly, Cao et al. (2009) suggested that high temperature from the heading resulted in a more considerable yield reduction in temperature-sensitive genotypes due to poor fertilization and low-speed setting. In contrast, the minimal effect was observed on female reproductive organs in rice. Spikelet fertility reduced significantly in sensitive genotypes, and this reduction was closely associated with germinating pollen on stigma and pollen tube length to the ovary (Jagadish et al. 2010a, b). A study performed by Nagarajan et al. (2010) in rice (basmati and non-basmati genotypes) under high temperature recorded a reduction of S.F. and yield/plant. Bahuguna et al. (2015) identified Nerica L44 (NL-44) for reproductive resilience, with better ROS managing ability, robust antioxidant enzyme system, and high spikelet fertility and grain yield in HS at flowering and vegetative stages.

4.6 Effect of Stress on Rice Grain Yield, Spikelet Fertility, and Pollen Viability

The HS stress is not the only factor responsible for reducing S.F., P.V., and grain yield; drought stress may be responsible for the decline. Mild drought at flowering resulted in a 70% reduction in secondary branching and decreased by 40% in spikelet fertility and panicle number (Kato et al. 2008). In maize, prolonged drought results in reduced sink size and grains number (Bahuguna et al. 2018; Barnabás et al. 2008; Aslam et al. 2013). Drought stress at anthesis results in increased improper anther dehiscence, ovary and pollen abortion, panicle exertion, lower spikelet fertility in rice maize and wheat (Rang et al. 2011; Powell et al. 2012; Praba et al. 2009; Aslam et al. 2013). Drought at pre-anthesis results in asynchronous flowering, or delayed flowering was recorded in wheat (Cattivelli et al. 2008; Foulkes et al. 2007).

The drought stress can affect panicle exertion and cause a reduction in spikelet fertility and grain yield in rice. O'Toole and Namuco (1983) reported that decline in spikelet fertility related to failure in panicle exertion from leaf sheath and matrix water potential of the flag leaf. Selote and Khanna-Chopra (2004) suggested that water stress can decrease spikelet fertility in sensitive rice high-yielding genotypes compared to N22 (tolerant). Various studies indicate that the reproductive stage comprises the microsporangium process for developing functional and viable pollen grains for fertilization and is most critical to stress. Under drought stress, structural and functional disparities create and lead to improper fertilization and seed setting (Saini and Westgate 2000). Pollen development processes like anther dehiscence and pollen shedding are also affected by drought stress (Ekanayake et al. 1990; Satake and Yoshida 1978). It suggested that in DS, sucrose transport to pollen represses, which results in lower P.V. in rice and other cereals (Powell et al. 2012). A similar drought result suggested that drought affects pollen viability during the pollen development stage (Kato et al. 2008; Dolferus et al. 2011). Lilley et al. (1996) and Ekanayake et al. (1993) also suggested that upland rice was more adapted to the water conserved mechanisms than others during drought spells. A greenhouse study performed by Rang et al. (2011) tested five genotypes to drought, found a significant decline in pollen count (52 to 70%), pollen on stigma (59%), and spikelet fertility by 81% in sensitivity genotypes, whereas tolerant (N22) have a lesser reduction in all above traits.

Sharma et al. (2018) performed a pot study in rice and phenotyped 15 rice cultivars by withholding irrigation at anthesis and drought were maintained at ~70 kPa and reported that P.V. (50%), S.F. (48%), and grain yield per plant and 1000 grain weight significantly affected under drought as compared to well-watered conditions. Bahuguna et al. (2018) reported that drought at flowering reduces spikelet fertility and grain yield/plant. They also recommended that priming at the critical stage helps in kick-start stress signaling and helps in developing acclimatize response against stress. The genetic diversity analysis performed on 296 Indica rice panels under drought stress also significantly reduced grain yield, spikelet fertility, 1000 grain weight, and spikelet number per panicle at 64 kPa and 45 kPa, respectively (Kadam et al. 2018).

4.7 Effect of High Temperature on Rice Grain Yield, Spikelet Fertility, and Pollen Viability

Some studies have reported combined effects of drought and high-temperatures stress and suggested that combined stress was much more detrimental than individual ones. Rang et al. (2011) indicated a decline in S.F. concerning particular stress and normal conditions. Lawas et al. (2019) reported a reduction of 73% yield due to combined high temperature and drought stress in sensitive genotypes compared to control ones.

4.8 Heat Susceptibility Index and Cumulative Stress Response Index

Fischer and Maurer (1978) categorized wheat genotypes in water deficit based on yield; they performed under drought stress and identified them according to their susceptibility index. In brief, the rate of change in yield between two environments relatively means a shift in overall genotypes. Later, Dai et al. (1994) and Koti et al. (2007) suggested the cumulative stress response index, all the sum of individual relative components response of treatment was the best way to identify the actual response of cultivars in any stress conditions.

4.9 Effect of High Temperature on Rice Seed Quality

Studying the HS effect on rice quality is essential for rice productivity and marketability. Rice's appearance, cooking, and texture are the main quality traits that are major concerns of consumers (Okabe 1979; Rousset et al. 1999). Various studies have suggested rice grain quality can be a more concerning issue in HS (Madan et al. 2012; Lyman et al. 2013). Most reports are available on control conditions studies (Fitzgerald and Resurreccion 2009; Lisle et al. 2000), and very few studies carried in field conditions. Heat stress at the grain filling and flowering stage can make an abnormal change in color and grain texture due to insufficient starch accumulation (Tsukaguchi and Iida 2008). The grain chalkiness was the major component in determining the rice price and quality.

Yoshioka et al. (2007) characterized conventionally chalky grains using image-based techniques in the white core, milky white, white back, and white belly rice. High temperature deteriorated quality traits like grain appearance hulling, milling yield, high chalkiness percentage, head rice recovery, amylose content which can affect market values of rice (Inatsu 1979; Cock et al. 1976). It may result from changes in the activity starch biosynthesis pathway and alteration in granules packing in rice grains (Tetlow and Emes 2014; Dai et al. 2005).

Head rice recovery is an essential trait for rice selection in West Africa (Sakurai et al. 2006). The study suggested that head recovery is affected by high air temperature and relative humidity (Cnossen et al. 2003; Schluterman and Siebenmorgen 2007). Cooper et al. (2008) suggested that high night temperature was also responsible for significantly reducing head rice yields. Nagata et al. (2004) indicated under high temperature at early grain filling and post-flowering was primarily accountable for rice grain fissuring, which resulted in the reduction of head rice yield. Under high-temperature stress, sink capacity is altered, resulting in lower starch synthesis activity and 1000 grain weight (Jeng et al. 2003; Oh-e et al. 2007). Grain chalkiness is another essential trait that determines rice quality and price in the international market. The high temperature at early grain filling and post-flowering affects the packing of starch granules and created air spaces. As a result, in grains chalky regions developed at maturity (Tashiro and Wardlaw 1991; Zakaria et al. 2002). These loose packing of amyloplasts in kernels results in the formation of chalky grain and differs from translucent grains (Lisle et al. 2000).

Rice grain mainly consists of two types of starch, i.e., amylopectin and amylose. Under normal conditions, amylose concerning amylopectin is responsible for the firmness of cooking grain (Juliano 1992; Blakeney et al. 1994). Under high-temperature reduction of amylose content increases amylopectin in rice grains (Umemoto et al. 2002; Asaoka et al. 1989; Umemoto and Terashima 2002). These changes in amylose content led to sticky rice after cooking (Sakurai et al. 2006) and are not favorable for consumption (Sakurai et al. 2006).

4.10 High Temperature Effect on Gaseous Exchange and Tissue Temperature

Photosynthesis rate (i.e., CO_2 uptake) and transpiration rate (i.e., H_2O loss) are regulated through the stomatal behavior of the plants. This stomatal pore opening and closing maintain the tissue temperature and moment of metabolites or signaling compounds in plants (Brownlee 2001; Lake et al. 2001).

Pn "(rate of photosynthesis)" is affected under high temperature and drought (Hassan 2006; Yordanov et al. 1999). The limitation in the rate of photosynthesis in DS and HS can occur either due to nonstomatal or stomatal attributes (Shangguan et al. 1999; Ort et al. 1994). Whichever limitation in gas exchange might limit plant growth and development in various stresses. Various researchers recommended that in high temperature and drought individually or in combination rate of photosynthesis and transpiration decline (Zandalinas et al. 2016; Arbona et al. 2013). In high temperatures, the reduction in yield in cereals is associated with carbon assimilation (photosynthesis and transpiration) (Stone 2001). High temperature resulted in a lower rate of photosynthesis because of (1) inactivation of Rubisco enzyme activity (Prasad et al. 2004) and (2) destruction of Photosystem II (PSII) (3) by the decreased rate of consumption of CO_2/O_2 and/or increased photorespiration in mesophyll cells (Leegood and Lea 1999). PSII is the most prominent high-temperature sensitive component (Gombos et al. 1994). Wise et al. (2004) recorded that HS stress carbon metabolism in the stroma and photochemical reaction in thylakoid lamella of the chloroplast are affected.

Various studies have suggested that high-temperature stress can cause degradation of chlorophyll a and b in the leaf of different crop species (Karim et al. 1999). In *Solanum Lycopersicum* and *Saccharum officinarum*, HS increased the chlorophyll a: b ratio and decreased chlorophyll:carotenoids ratio in the least susceptible genotypes (Camejo et al. 2005; Wahid and Ghazanfar 2006). Such chlorophyll degradation or photosynthesis apparatus has been associated with ROS production (Guo et al. 2006). The rate of photosynthesis is affected under high temperatures due to disruption of the thylakoid membrane or inhibiting membrane-associated electron carriers and enzymes (Rexroth et al. 2011). More than 35 °C decreased the activity of Rubisco and can limit the photosynthesis system in various plants (Griffin et al. 2004). Zhang et al. (2018) reported lower photosynthetic rate ($P_{.N.}$) insensitive rice genotypes as compared to N22 under heat stress. Similarly, reduction in Rubisco activity in rice and wheat study has been suggested as a cause of lower $P_{.N.}$ in HS (Perdomo et al. 2017)

In drought stress, stomatal conductance decreases and ultimately reduces CO_2 flow in mesophyll cells. Similarly, reduction in the activity of RuBP (Ribulose biphosphate) (Parry et al. 2002) or Rubisco content (Bota et al. 2004) can affect the rate of photosynthesis under drought stress. Speer et al. (1988) reported that drought stress caused instability to the photosynthesis membrane via dehydration in later stages on the plasma membrane. Chaves et al. (2011) suggested that under severe DS, de novo synthesis of photosynthesis proteins slows down, which adversely affects the photosynthesis capacity and enhanced leaf senescence.

4.11 Effect of High Temperature on Relative Water Content (R.W.C.)

Relative water content (R.W.C.) is a critical trait that showed the degree of hydration in tissue and cell and is an essential feature in better growth and physiological functioning (Silva et al. 2007). Blokhina et al. (2003) suggested that plasma membrane permeability and suitability decreased due to dehydration under drought stress. Vendruscolo et al. (2007) indicated that tolerant varieties maintain R.W.C. concerning sensitive ones under water deficit environments. Those varieties keep relative water content-maintained protoplasm under water stress and ensure yield in rice (Sikuku et al. 2012).

4.12 Effect of High Temperature on Membrane Stability Index (MSI)

The membrane integrity defines the permeability or integrity of the plasma membrane (Blokhina et al. 2003). Under stress conditions, plasma membrane permeability increases and increases "electrolytes leakage" from the stress-imposed tissue (Chaturvedi et al. 2012). This electrolytic leakage can be addressed as electrolytic conductance (Agarie et al. 1995). Swapna and Shylaraj (2017) suggested that tolerant varieties have better MSI under drought stress conditions as compared to sensitive ones.

4.13 Effect of High Temperature on Reactive Oxygen Species and Antioxidant System

Under adverse environmental stress conditions, plants activate various types of defense mechanisms in genes, proteins, and signaling cascades to confer tolerance. These stress conditions are liable for the generation of ROS in the organism. ROS act as double-edged sword nature molecules in lower concentration by acting as signaling compounds, whereas in higher it was malevolent nature (Noctor et al. 2014; Baxter et al. 2014). A report summarized ROS as harmful molecules which were highly reactive to nucleic acid, proteins, lipids, and other metabolites (Gill and Tuteja 2010a, b). These ROS molecules comprise various molecules, namely H_2O_2 oxide radicals ($O•_2-$, OH•, singlet oxygen, and many others). Many reports have suggested that ROS overproduction caused toxicity to nucleic acid, protein, and other metabolites, resulting in cell death and damage (Gill and Tuteja 2010a, b). Under natural conditions balance of ROS and the scavenging mechanism is there, but under stress conditions, this balance gets disturbed and caused cellular damage (Das and Roychoudhury 2014). Szymańska et al. (2017) proposed a robust defense mechanism (antioxidant defense) in maintaining ROS levels under detrimental limits. As ROS activity increased, during HS and D.S., which will possibly affect in peroxidation of lipids and disturbing the integrity of the plasma membrane.

The ROS scavenging components are presented in both enzymatic and non-enzymatic forms. Researchers reported that under drought stress conditions, the expression of enzymatic antioxidants increased in rice (Fahramand et al. 2014) which include S.O.D. (superoxide dismutase), C.A.T. (catalase), A.P.X. (ascorbate peroxidase), G.P.X. (guaiacol peroxidase), G.R. (glutathione reductase), and others (Sahebi et al. 2018), while non-enzymatic are A.A. (ascorbic Acid), G.S.H. (reduced glutathione), α-tocopherol, carotenoids, flavonoids, and proline (Boukar et al. 2019). Abiko et al. (2005) suggested that tolerant plants protect themselves from the harmful effect of ROS by synthesizing antioxidants components. These antioxidants are located at various organs of cells and collaborate to detoxify reactive oxygen species. You and Chan (2015) suggested that in all the enzymatic antioxidants, S.O.D. are the primary defense line of defense which convert O_2•- into H_2O_2 then C.A.T., G.P.X., and A.P.X. play key role in detoxification of H_2O_2 (You and Chan 2015). It has been shown that ascorbic acid is required for A.P.X. activity while glycol for G.P.X. (Noctor et al. 2014; Dietz et al. 2006; Meyer et al. 2012). Several studies reported that in the rice genome, eight S.O.D. genes encoded viz. one Mn-SOD (manganese S.O.D.), CuZn-SOD (plastidial S.O.D.), CuZn-SOD-L (putative CuZnSOD-like) and 2 copper-zinc S.O.D, cytosolic (cCuZn-SOD1 and cCuZn-SOD2) and iron S.O.D.s (Fe-SOD2 and Fe-SOD3) (Nath et al. 2014). Sharma and Dubey (2005) demonstrated an upregulated activity of S.O.D. in *Oryza Sativa* L. in water deficit stress. Bahuguna et al. (2015) demonstrated a rise in activity S.O.D., A.P.X., and G.P.X. of tolerant genotypes under high temperature in rice in both vegetative and spikelets and helped minimize high-temperature stress levels. The various transgenic approaches also justified that under-stress overexpression of Mn-SOD1 reduces stress induction (Li et al. 2013). Teixeira et al. (2004, 2006) reported 8 APX genes in rice. Two mitochondrial A.P.X.s (OsAPX5 and OsAPX6), two peroxisomal A.P.X.s (OsAPX3 and OsAPX4), two cytosolic A.P.X.s (OsAPX1 and OsAPX2), and two chloroplastic A.P.X.s (OsAPX7 and OsAPX8) and two cytosolic A.P.X. genes have a crucial role in abiotic stress tolerance (Zhang et al. 2013; Sato et al. 2011) rice. Several researchers proposed under high-temperature stress condition ROS like H_2O_2, hydroxyl radicals produces at PSII system was scavenge by antioxidant including S.O.D. In signal transduction, the involvement of ROS implies the intensity of stress and to maintain ROS at nontoxic levels, there must be a synchronized function of the regulatory network in balancing ROS production.

Hussain et al. (2019) suggested that in combined HS and DS conditions, metabolites accumulation and enzymatic and non-enzymatic antioxidants increased to prevent oxidative damage in maize. Zhang et al. (2018) suggested similar in rice anthers under high temperature.

4.14 Osmolytes Accumulations in High Temperature and Drought

The critical adaptation for many kinds of cereal under abiotic stress, i.e., heat and drought, is the accumulation of specific low molecular mass organic molecules called osmolytes. Under stress conditions, these osmolytes are accumulated in plants to regulate stress tolerance. Common examples of these osmolytes are sugar, proline, glycine betaine, tertiary and quaternary ammonium compounds, and tertiary sulfonium compounds.

Amphoteric quaternary amine, glycine betaine (G.B.), has a vital role as compatible solutes in various plant abiotic stresses, especially in high temperatures and drought. The glycine betaine content varied from species to species under stress conditions. In maize, it has been reported that more accumulation of G.B. enhances the stress levels under high temperature and drought stress conditions. It was previously reported that it helps improve photosynthesis rate in individual heat and drought and combine stress in wheat. Under water scarcity, it has been reported rise in the level of G.B. in maize and sugarcane (Wahid 2007). It has also been suggested that a rise in temperature by 4–5 °C PSII efficiency inhibited and leads to the accumulation of G.B., which was reported to protect the PSII system from photoinhibition in high-temperature stress. In high-temperature stress, CO2 fixation was affected, resulting in the generation of ROS, G.B. stabilized the Rubisco, resulting in a reduction in ROS generation in crops.

Like glycine, proline is also a critical osmolyte, which accumulates in large quantities under environmental stress conditions. Proline is synthesized from glutamate by the action of two enzymes, Δ1-pyrroline-5-carboxylate synthetase and Δ1-pyrroline-5-carboxylate reductase. It was known that proline also regulates the cellular redox potential under stress environments, exceptionally high temperature, and drought stresses. It also has various functions, such as signaling molecule, a metal chelator, and antioxidant defense. High temperature showed its first presence at the cellular level, especially at the plasma membrane, affecting biochemical events. Kumar et al. (2016) suggested that under high temperature rise in proline content was noted. Under high temperatures, fruit set in tomato plants failed due to disrupting sugar metabolism and proline transport during the narrow window of male reproductive development. Hexose sensing in transgenic plants engineered to produce trehalose, fructans, or mannitol may significantly contribute to the stress-tolerant phenotypes.

Trehalose is a non-reducing disaccharide of glucose that functions as a compatible solute in stabilizing biological structures under abiotic stress in bacteria, fungi, and invertebrates. Trehalose also acts as a storage carbohydrate, and it possesses the unique feature of reversible water absorption capacity to protect biological structures from damage during drought and high temperatures. When water dissipates from the shell of macromolecules (such as protein) during severe dehydration, trehalose can act as a water substitute on the surface of the dried protein. Thus, proteins' native folding and biological activity are maintained, and denaturation and aggregation are prevented. A study revealed that upregulation of trehalose biosynthetic genes in rice has considerable potential for improving abiotic stress tolerance and, at the same time, augmenting productivity under both stress and non-stress conditions. It suggested that from overexpression of trehalose in a higher capacity for photosynthesis and a concomitant decrease in the extent of photo-oxidative damage during stress. In addition, trehalose must be interacting with other physiological processes to account for changes in ion uptake and partitioning during salt stress. Because other cereal crops, like rice, are also sensitive to abiotic stresses, likely, overexpression of trehalose biosynthetic genes in maize and wheat may also confer high levels of abiotic stress tolerance.

4.15 Hormone Metabolism in High-Temperature Stress

Crops are very susceptible to these changing environmental conditions. To overcome these harmful and adverse conditions, phytohormone, plays a key role, whose signaling helps the plants to adapt and survive under these stress conditions. These are part of key metabolic pathways that help sustain plants and control the yield components (Peleg and Blumwald 2011). Some basic phytohormones are classified into five standard groups viz. ethylene (E.T.), Abscisic acid (A.B.A.), auxin (I.A.A.), gibberellins (G.A.), and cytokinins (C.K.) were mainly present.

Under abiotic stress, crosstalk between hormones develops synergetic or antagonistic relations, which plays a pivotal role in plant development processes. Previous research suggested that auxin (I.A.A.), cytokinin (C.K.), and gibberellic acid (G.A.) are involved in plant development and regulate the response to stress environments (Eyidogan et al. 2012). Zhang et al. (2009) suggested that auxin regulation in modulating the drought response. Likewise, A.B.A. is involved in regulating stomatal closure to prevent water loss to minimize transpiration and decrease growth under drought stress (Schroeder et al. 2001). Xue-Xuan et al. (2010) reported that A.B.A. signaling plays an essential role in developing plants' drought and cold stress tolerance. E.T. is a gaseous hormone regulating process involving various stages of growth phases, viz. leaf, petals abscission, flower senescence, and fruit ripening and developed in abiotic stress response (Abeles et al. 2012).

Another newly identified group of chemical groups are nitric oxide (NO), salicylic acid (S.A.), strigolactone (S.L.), brassinosteroids (B.R.), jasmonate (J.A.), and polyamines (PAs). In all above, PAs (polyamine) are newly class molecules that play a crucial role in plant development and response under abiotic stresses conditions (Minocha et al. 2014). In various observations, PAs different concentrations were noted during “plant growth and development” and were correlated to “different stresses at cellular levels.” The polyamines are reported for various adaptation and acclimation mechanisms to cope with different stress conditions (Pál et al. 2015; Karwa et al. 2020). Liu et al. (2007) suggested that polyamines act as a secondary messenger in a common signal transduction pathway in *Arabidopsis thaliana*. Various early and recent work told that PAs have crosstalk with various other hormones viz. gibberellins, auxin, and ethylene for maintaining different processes, but their pronounced relation is not establishing the interaction and mechanism of such crosstalks (Kusano et al. 2008; Alcázar et al. 2010; Bitrián et al. 2012; Xu et al. 2014).

4.16 Conclusion

As the rice is the source of nutrition to the large population of the world, the increasing high-temperature spikes and drought spell the demand for resilient rice varieties rises. Lack of knowledge, how plants can sense and cope up these harsh environments, physiological and biochemical traits which at par correlate with yield and quality traits that can also help us to identify the most important one under these stresses. Under the stress condition, plant either showed tolerant, escape, or avoiding the mechanism for which either it regulates the tissue temperature or by early flowering traits it avoids the high temperature and drought spells. There are various noticeable effects of high temperature and drought is observed on pollen viability, affected grain filling, structural changes of cell organelles, oxidative stress, lipid peroxidation of cell membranes, disruption of leaf water relations, and reduction in photosynthesis. All these effects regulate the water potential, membrane permeability, and osmolytes regulation, which can help in restricting the water losses under stress conditions. Hormone regulation helps in generating the systemic signaling pathway which regulates the H_2O_2 content and HSPs that help in proper regulation of photosynthesis and transpiration process under stress conditions.

In the future, efforts are needed to phenotype large genotypic variability on the basis of early flowers opening traits and by maintaining spikelet fertility, cell membrane thermostability, photosynthesis, transpiration, HSPs, and maintaining a greater non-structural carbohydrate pool under high temperature and drought stress. A challenge for the future is to achieve the robust tolerant mechanism that can help the plant to sustain high temperature and drought stress environments in climatic change scenarios.

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