REVIEW ARTICLE Agricultural Reviews, Volume 45 Issue 1: 115-120 (March 2024)

Heat Tolerance and Effect of High Temperature on Floral Biology and Physiological Parameters in Rice: A Review

Vanitha Jayaraman[1], Mahendran Ramachandran[1]

10.18805/ag.R-2353

ABSTRACT

Rice (*Oryza sativa* L.) is one of the major cereal staple food crops consumed by more than 50 per cent of the world's population. Due to global climatic changes, the crop has to withstand higher temperatures in the near future. In India, rice cultivation is more affected by climate change and it contributes to yield loss and in severe cases results in crop failure both of which leads to economic losses. Grain yield declined by 10% for each 1°C increase in minimum temperature in the dry season whereas the effect of maximum temperature was insignificant. Significant variation exists among rice germplasm in response to high temperature stress. Producing an economically significant yield under heat stress conditions depends on floral biology of rice and several plant physiological parameters and mechanisms that contribute to heat tolerance in the field, such as photosynthesis, chlorophyll content, canopy temperature depression and concomitant increases of transcripts coding for proteins involved in protection. According to the objectives of this study, the literature pertaining to the aspects of heat tolerance and effect of high temperature on floral biology and physiological parameters in rice is briefly reviewed.

Key words: Floral biology, Heat tolerance, Physiological parameters, Rice.

Heat tolerance and effect of high temperature on floral biology of rice

Rice is extensively grown in irrigated cropping system, allowing production in the warmer, high radiation post-monsoon and summer months. Rice production has also intensified in rainfed-lowland and dry land (upland) cropping systems, many of which are prone to drought and high temperature (Coffman, 1977). Flowering (anthesis and fertilization) and to a lesser extent booting (microsporo genesis) are the most susceptible stages of development to temperature in rice (Satake and Yoshida, 1978; Farrell *et al*., 2006) which can induce floret sterility and limit grain yield (Osada *et al*., 1973; Satake and Yoshida, 1978 and Matsushima *et al*., 1982). Since the 1980's an increase in the concentration of greenhouse gases, such as carbon-di-oxide in the atmosphere is thought to have been responsible for an increase in the air temperature (Hansen *et al*., 1984). Amongst other issues, global warming is expected to result in the occurrence of high temperature induced floret sterility in rice.

Heat tolerance studies in rice are an emerging area of research and only limited literatures are available. Crop scientists have attempted to assess the effects of increasing temperature in the atmosphere, on the growth and yield of rice and also examined the relationship between morphological characteristics of the anther and floret tolerance to high temperature at flowering in rice cultivars in relation to sterility. Matsui *et al.* (2000) studied the effect of high temperature at flowering on the ability of thecae to dehisce and also on pollen-grain swelling which causes thecae dehiscence. Two japonica cultivars grown under submerged soil conditions were subjected to high (39°C) and moderate (34°C) temperature from 10 am to 4 pm for three consecutive days at the flowering stage.

[1]Sri Ramaswamy Memorial Institute of Science and Technology, Chengalpattu-603 203, Tamil Nadu, India.

Corresponding Author: Vanitha Jayaraman, Sri Ramaswamy Memorial Institute of Science and Technology, Chengalpattu-603 203, Tamil Nadu, India. Email: vanithaj@srmist.edu.in

How to cite this article: Jayaraman, V. and Ramachandran, M. (2024). Heat Tolerance and Effect of High Temperature on Floral Biology and Physiological Parameters in Rice: A Review. Agricultural Reviews. 45(1): 115-120. doi: 10.18805/ag.R-2353.

Submitted: 25-08-2021 **Accepted:** 10-02-2022 **Online:** 28-03-2022

Prasad *et al.* (2006) studied the effect of ambient and high temperature on spikelet fertility in fourteen rice cultivars of different species (*Oryza sativa* and *Oryza giaberritna*), ecotypes (*indica* and *japonica*) and origin (temperate and tropical). They observed that high temperature significantly decreased the spikelet fertility across all cultivars, but the effect varied among cultivars (Baidya *et al.* 2020). Based on the decrease in spikelet fertility at high temperature, cultivar N22 was adjudged as most tolerant, while the cultivars L 204, M 702, Labelle, Italica Livorna, WAB 12, CG 14 and CG 17 were highly susceptible and the cultivars M 103, S 102, Koshihikari, IR 8 and IR 72 were moderately susceptible to high temperature. Decreased spikelet fertility and cultivar difference at high temperature was mainly due to decreased pollen production and pollen reception. Lower spikelet fertility at elevated temperature resulted in fewer filled grains. They concluded that spikelet fertility at high temperature can be used as a screening tool for heat tolerance during the reproductive phase. The effect of high temperature in Pusa 44 during vegetative, reproductive and ripening growth phases were observed; its growth, yield and yield components were studied by Singh *et al.* (2006).

They witnessed that compared to the crops grown in normal conditions, those exposed to heat stress during their vegetative and reproductive growth phases had development of their sink potential impaired *i.e.*, lesser number of panicles m^{-2} and number of spikelets^{-1}. The stress during grain filling stage did not show any detrimental effects on sink development, rather impaired sink potential realization by reducing the number of grains panicle^{-1}.

Jagadish *et al.* (2007) studied the effect of high temperature at anthesis on spikelet fertility in IR 64 (lowland *indica*) and Azucena (upland *japonica*) at 29.6°C (control), 33.7°C and 36.2°C temperatures. In IR 64, high temperature increased the number of spikelets reaching anthesis, whereas in Azucena the spikelet numbers were reduced. In both genotypes <1 h exposure to >33.7°C at anthesis caused sterility. In IR 64 there was no interaction between temperature and duration of exposure, spikelet fertility was reduced by 7% per °C at >29.6°C. In Azucena, there was a significant interaction and spikelet fertility was reduced by 2.4 per cent °C/d above a threshold of 33°C. They concluded that marking individual spikelets is an effective method to phenotype, genotypes and lines for heat tolerance that removes any apparent tolerance due to temporal escape.

The morphology of reproductive organs and pollen number in response to high temperature at anthesis in three rice (*Oryza sativa* L.) genotypes was reported by Jagadish *et al.* (2010). Plants were exposed to 6 hours of high (38°C) and control (29°C) temperatures at anthesis and spikelets were collected for morphological analysis. They observed significant differences among the genotypes in anther length and anther width, apical and basal pore area and stigma and pistil length. Temperature also affected some of the other traits like increasing anther pore size and reducing stigma length.

Rang *et al.* (2011) studied the effect of high temperature and water stress on pollen germination and spikelet fertility in N 22, IR 64, Apo and Moroberekan. Plants were exposed to high temperature and water stress during flowering to quantify their response through spikelet fertility. They observed strong relationship between spikelet fertility and number of pollens geminated on stigma. In N 22, there was better anther dehiscence, higher *in vitro* pollen germination and higher spikelet fertility indicating its ability to tolerate multiple stresses.

High temperature stress is one of the most important environmental factors influencing crop growth, development andyield processes. Shrivastava *et al.* (2012) studied the effect of high temperature at different growth stages on rice yield and grain quality traits. They witnessed paddy length was the only trait which exhibited high broad sense heritability under all the dates of sowing and for quality traits highest heritability was observed for length of brown rice, length of milled rice, amylose content, head rice recovery and protein content. Based on overall results of head rice recovery and grain yield of RF-79 and Samleshwari was identified to be the best genotype under high temperature conditions.

Tenorio (2013) screened 455 IRRI Gene bank accessions from hot rice growing regions during hot season and 200 accessions with high spikelet fertility were selected for phenotyping in temperature-controlled outdoor growth chambers with 38/21°C day/night temperature and 70/75 per cent day/night relative humidity (RH). From the 200 accessions, 28 were selected and reconfirmed along with 12 potential heat-tolerant accessions from IRRI breeding programs. Finally, 23 accessions were selected as potential donors for heat tolerance and also evaluated by exposing them to controlled high temperature during booting and flowering stages. High-temperature treatment of 39°C is suitable for screening heat tolerance at booting stage, while 38°C is suitable for flowering stage evaluation.

Manigbas *et al.* (2014) studied the germplasm innovation of heat tolerance in rice for irrigated lowland conditions in the Philippines. In this study, phenotype and desirable material selection from various crosses were performed under high temperature conditions during the reproductive stage. Screening was performed in the field and glasshouse to select individuals with heat tolerance and high yield potential. They identified several advanced breeding lines from Gayabyeo/N22 cross produced desirable individuals with heat tolerance, resistance to pests and diseases and high yield potential.

Phenology is the most important factor in determining the grain yield under stress condition (Shrivastava *et al.*, 2012). When evaluating the usefulness of traits to increase grain yield, it is important to consider phonological development, which have an overriding effect on the grain yield under high temperature condition (Wassmann *et al.*, 2009).

The reproductive development in plant is highly vulnerable to heat stress (Jagadish *et al.*, 2012). Earlier days up to fifty per cent flowering are advantageous for the retention of more green leaves at anthesis under high-temperature conditions, leading to a smaller reduction in yield (Tewolde *et al.*, 2006).

Time of flowering and anthesis is the most important traits for identifying high temperature tolerance genotypes under heat stress condition. Flowering and anthesis in most O. *sativa* genotypes of rice occur over a 5-day period, with most spikelets reaching anthesis between 10:00 h and 12:00 h (Nishiyama and Blanco 1980; Prasad *et al.* 2006). A rice floret emerges from the sheath of the flag leaf just before anthesis and opens for about 1 h in the morning (Matsui *et al.*, 2005). Avoidance mechanisms includes: (i) cooling of the spikelet at flowering, (ii) asynchronous tiller and panicle development, (iii) asynchronous flowering time of spikelets within each panicle and (iv) anthesis and pollination taking place within the same spikelet (self-pollination). The latter was considered as one of the major differences between heat-tolerant (N22) and susceptible variety Improved White Ponni. Similar results were reported by Yoshida, (1981). Yield depression as a result of exposure to high temperatures during critical developmental stages is mitigated to some extent within a crop because it is composed of individuals whose tillers are not of the same

age. This means that the panicles produced pass through their vulnerable stages at different times and some might therefore escape heat damage. However, breeders and growers do not want crops to be unreasonably asynchronous as this extends the ripening period and increases the risk of crop loss due to other factors. The anthesis time during the day is important because spikelet sterility is induced by high temperature during or soon after anthesis (1-3 h after anthesis in rice, Satake and Yoshida 1978), but not after fertilization is completed. Sheehy *et al*. (2001) showed that a large variation exists in time-of-day of flowering among rice cultivars. Identification of genes responsible for controlling the time of day when flowering commences would be crucial for this stress avoidance mechanism (Sheehy *et al.* 2005).

Number of total tillers is the most important trait related to yield. The vegetative phase is divided into two subphases: (i) the active-vegetative phase that lasts to maximum tillering and is accompanied by a rapid increase in plant height, tiller number and dry-matter production. (ii) vegetative-lag phase continues up to panicle initiation. During the vegetative-lag phase, maximum tillering, internode elongation andpanicle initiation occur almost simultaneously in cultivars with 105-120 days duration and successively later in cultivars with more than 140 days duration. The physiological growth stage is generally indicated by the number of fully developed leaves on the main stem (De Datta, 1981). The reproductive phase, which is characterized by the culm elongation, emergence of the flag leaf, booting, heading and filling of the spikelets; begins just before or after the maximum tillering. Temperature affects the growth duration of the rice crop to a great extent. When rice is exposed to high air temperatures during the vegetative stage, individual plant height, tiller number anddry weight may be considerably reduced (Krishnan *et al*., 2011).

Flowering is the most sensitive stage to high temperature in the rice life cycle (Satake and Yoshida, 1978; Sato, 1979). High temperature of over 35°C at flowering stage increases pollen and spikelet sterility, which leads to significant yield losses, low grain quality and low harvest index (Osada, 1973; Matsushima, 1982 and Matsui, 1997). Spikelet sterility is one of the most important traits for determining the yield response of resistant genotypes. The same result was obtained in our study that the susceptible parent, improved white ponni had high spikelet sterility percentage and rachis wise sterility per cent when compared to high temperature tolerant genotype like N22 in both open and shade condition (Ishimaru *et al.,* 2010). N22 had low spikelet sterility percentage and rachis wise sterility per cent when compared to other genotypes which might be due to the changes in carbohydrate levels and enzyme activities associated with inhibition of starch accumulation in pollen (Sheoran and Saini, 1996).

Large cultivar variation exist in the spikelet sensitivity to high temperature damage andthe primary cause of this cultivar variation in high temperature (heat) tolerance at flowering is the number of viable pollen grains shed on the stigma, resulting from the changes in the extent of anther dehiscence (Matsui and Omasa, 2002) which directly affect the spikelet fertility and grain yield (Matsui *et al*., 1997). Thus, spikelet fertility under high temperature has been widely used as a screening index for heat tolerance at reproductive stage Prasad *et al*. (2006). In recent years, rice varieties tolerant to high temperature have been identified by Matsui *et al*., 1997; Prasad, 2006 and Tenorio (2013).

Hundred grain weight serves as a major selection parameter for yield improvement in rice under heat stress. High or low temperatures at meiosis stage affect the seed-setting rates. With the increase of temperature and its duration, the seed-setting rate decreases gradually. The relationship between daily relative seed-setting rate and temperature can be fitted with a quadratic equation. However, total effect of high temperature during meiosis stage can be described by the products of these daily relative seed-setting rates (Shi *et al*., 2008). Heat stress during meiosis influences the development of anther and pollen grains, significantly reducing anther dehiscence, pollen fertility rate and yield components such as number of spikelets per panicle, seed-setting rate, 1000-grain weight and grain yield (Cao *et al*., 2008). However, Murata (1976) observed that the 1000-grain weight of the same variety varied from about 24 g at a mean temperature of 22°C in the 3-week period after heading to 21 g at a mean temperature of 28°C.

Biomass is one of the most important traits for determining the yield responses of tolerant genotypes. Although high temperatures can stimulate plant growth to some extent, they also speed up development thus shortening the life cycle. Under high temperatures, tissues and organs have less time to acquire photo assimilates, which can result in fewer and/or smaller organs leading to less biomass accumulation.

Total dry matter production is one of the selection criteria for identifying heat tolerant genotypes under heat stress condition. There are significant decreases in grain dry weight increases in temperatures during the period of grain development (Tashiro and Wardlaw, 1991a). The greatest change in dry weight of the grains takes place when heat stress in grains occurs during the linear phase of dry matter accumulation.

Grain length/breadth serves as a major selection parameter for yield improvement in rice under heat stress. Interestingly, the flow of nitrogen into grains is more stable than that of carbon as temperatures are increased. High temperatures interfere with the early stages of cell division and development in the endosperm. Grain length and breadth are affected when high temperatures occur earlier in development. Abortive and opaque grains are numerous when high temperature commenced 4 days after heading (Tashiro and Wardlaw, 1991b). Depending on both the temperature level and duration, chalky endosperm tissue occurs in several forms: white-core kernels are evident at a temperature of 27/22°C and white-back kernels are most numerous at 36/31°C when high-temperature stress occurs 16 days after heading.

Grain filling is one of the most important traits for determining the yield response of resistant genotypes for high temperature stress. Extreme high day temperatures during the grain-filling period may reduce starch synthesis in the grains, especially under N-deficient conditions (Ito *et al.*, 2009). High temperatures may also induce an accumulation of sucrose and a decrease in carbon and nitrogen transport from the shoots to the ears *via* the phloem. The enzymatic activity of starch synthesis is closely related to the formation and filling of grains (Jeng *et al.*, 2003). Shortening of the ripening period in rice due to high temperature is caused by higher activity of enzymes involved in starch synthesis during the early grain growth stage (Ohe *et al.*, 2007).

Grain yield is a major selection parameter for heat stress. Temperature influences rice yield by directly affecting the physiological processes involved in grain production. During the reproductive stage, the spikelet number per plant increases as the temperature drops. In general, the optimal temperature shifts from high to low as growth advances from the vegetative to the reproductive stages. As early as 1958, Matsushima and Tsunoda reported that the mean optimum temperature for ripening of japonica rice in Japan was about 20-22°C. Although temperature during ripening affects the weight per grain, the 1000-grain weight of a particular cultivar is considered to be almost constant under different environments and cultural practices.

Physiological parameter related to high temperature stress

Chlorophyll content and photosynthetic rate are important physiological parameters in plants. Heat stress directly affects photosynthesis in rice. Photosynthetic rates are higher during reproductive stage than the vegetative stage. Photosynthetic duration is controlled by the requirement of assimilates in the growing organs (*e.g.*, leaves) and the reproductive organs (*e.g.*, panicle) (Wassmann and Dobermann, 2007) and also by the environment.

Generally, tolerance to heat is characterized by a lesser effect on essential processes such as photosynthesis and by consistent increase of transcripts involved in the biosynthesis of protective components. As photosynthesis and reproductive development are the most sensitive physiological processes to stress (Prasad *et al.*, 2008), a heat-tolerant variety will be usually characterized by higher photosynthetic rates reflected in stay green leaves, increased membrane, high temperature stability and successful fruit set under high temperature conditions (Nagarajan *et al.*, 2010; Scafaro *et al.*, 2010 and Bita and Gerats, 2013).

Weerakoon *et al.* (2008) reported that transpiration cooling is one of the high temperature avoidance mechanisms and is better equipped to withstand high day temperature provided that sufficient water is available. Egeh *et al.* (1992) reported in a field study at the experimental farm of the IRRI, Philippines, subjected four rice genotypes (N 22, IR 52, IR 20 and IR 46) to high temperature using open top plastic chambers at 30 days after transplanting and investigated the temperature response of gas exchange traits. Transpiration rate, leaf conductance andintercellular CO_2 were greater for N22 than for the other genotypes at 41/33°C that contributed to the high-temperature tolerance of N22.

Alkhati and Paulsen (1999) observed that temperature had no effect on stomatal conductance and internal (CO_2) in rice, suggesting the non involvement of stomatal effects on changes in photosynthetic rates with temperature. The response of photosynthesis to heat stress is related to temperature dependence of Rubisco to the two substrates, carbon dioxide and oxygen. At high temperatures, the solubility of oxygen is decreased to a lesser extent than CO_2, resulting in increased photorespiration and lower photosynthesis (Lea and Leegood, 1999).

Matsui *et al.* (1997) studied the interaction of CO_2 and temperature at reproductive stage, recorded an increase in canopy temperature due to stomata closure at high CO_2 concentrations. They concluded that the critical air temperature for spikelet sterility (as determined from the number of germinated pollen grains on the stigma) was reduced by 1°C at elevated concentrations of carbon dioxide (ambient + 300 ml^{-1} CO_2) which could have been due to low transpiration cooling majorly driven by stomata closure. Increasing temperatures from 28/21 to 37/30°C decreased grain yield from 10.4 to 1.0 Mg ha^{-1} even under 660 mmol of CO_2 mol^{-1} of air.

High canopy temperature difference (CTD) has been used as a selection criterion to improve tolerance to heat (Ayeneh *et al.*, 2002 and Reynolds *et al.*, 2001) and has been associated with yield increase among cultivars (Fischer *et al.*, 1998). The suitability of CTD as an indicator of yield and stress tolerance, must be determined for individual environments. For example, it can be a poor indicator where yield is highly dependent on limited amounts of soil-stored water (Balota *et al.*, 2008). Vapour pressure deficit has a large effect on CTD, while net radiation, air temperature andwind speed have slight effects (Smith *et al.*, 1986). CTD effected by biological and environmental factors like water status of soil, wind, evapotranspiration, cloudiness, conduction systems, plant metabolism, air temperature, relative humidity and continuous radiation (Reynolds *et al.*, 2001), has preferably been measured in high air temperature and low relative humidity because of high vapour pressure deficit conditions (Amani *et al.*, 1996).

It was also observed that CTD has been used as a selection criterion for tolerance to high temperature stress in a breeding program. The breeding method used generally comes with mass selection in early generations like F_3. According to this method, firstly, bulks which show high CTD value (have cool canopy) were selected in F_3 generation. Later, single plants which show high stomata conductance (g) with cool canopy among bulks at the same selection generations, were used in high temperature breeding program (Reynolds *et al.*, 2001).

Generally, increase in temperature leads to reduction in carboxylation reduced activity of enzymes system, increased rate of transpiration and respiration (Egeh *et al.*, 1992). There is an every chance of altered metabolism under

high temperature and influence is evidenced in the case of root biology leading to less absorption of water and consequent rise in the leaf temperature. All the phenomena lead to the overall reduction in many of the vital morphological and subsequent physiological parameters. Rice plants when exposed to high temperatures during critical stages can avoid heat by maintaining their microclimate temperature below critical levels by efficient transpiration cooling. Moreover, the effect of high temperature is closely related to the ambient relative humidity and hence the level of transpiration cooling is determined by temperature and vapour pressure deficit. Stomatal conductance is the speed at which water evaporates from pores in a plant andis directly related to relative size of the stomatal aperture. Higher the evaporation rate, higher the conductance of the leaf.

CONCLUSION

Several approaches should be actively exploited to improve high temperature tolerance in current cultivars, including discovery and exploitation of new genes and alleles, improved breeding efficiency and marker assisted selection. Till date, there is no systematic study on monitoring and evaluation of temperature stress induced yield losses worldwide, although some sporadic reports on regional high temperature damages were documented in tropical and subtropical countries.

Conflict of interest

All authors declared that there is no conflict of interest.

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