Bulletin of Environment, Pharmacology and Life Sciences
Bull. Env. Pharmacol. Life Sci., Vol 7 [11] October 2018 : 162-169
©2018 Academy for Environment and Life Sciences, India
Online ISSN 2277-1808
Journal's URL:http://www.bepls.com
CODEN: BEPLAD
Global Impact Factor 0.876
Universal Impact Factor 0.9804
NAAS Rating 4.95

REVIEW ARTICLE **OPEN ACCESS**

Effect of Temperature on Different Growth Stages and Physiological Process of Rice crop- As a Review

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ABSTRACT
The atmospheric CO_2 concentration is expected to rise from 380 mmol mol^{-1} currently to between 485 and 1000 mmol mol^{-1}. As the consequence of greenhouse effect of many atmospheric trace gases including CO_2, warming of Earth will occur all the more. In the past 150 years, the global average surface air temperature has increased significantly by 0.15 0.05 °C per decade. The most of the rice is currently cultivated in regions where temperatures are already above the optimal for growth (28/22 °C); therefore, any further increase in mean temperature or episodes of high temperatures during sensitive stages of the crop may adversely affect the growth and yield of rice. Yield decrease was about 7–8% in rice for each 1 °C increase in daytime maximum/nighttime minimum in temperature from 28/21 to 34/27 °C. Moreover, the increase in temperature will eliminate the likely benefits of projected rise in atmospheric (CO_2) on rice plants. The thermal stability of cell membrane is considered to be positively associated with yield performance. Temperature is a major factor for photosynthesis. But, excessive temperatures can result in a decline in foliar photosynthesis and also a decrease in allocation of dry matter to shoots and roots. The adverse effects of high air temperature are not limited to the aboveground portion of rice. As the temperature of floodwater and soil get altered due to high air temperature, the below-ground portion can be equally, if not more affected. This review highlights the global significance of rice, the effects of high temperature due to climate change on growth and development, and yield components of rice and the need for future research studies.
Keywords- *CO_2, Temperature, Global Warming, Rice*

Received 12.07.2018 Revised 20.08.2018 Accepted 10.09.2018

INTRODUCTION

Globally, the harvested area of rice has increased only marginally from 120.1 million ha in 1960 to 155.7 million ha in 2008 [6] while the average rice yield has doubled from 1.84 to 4.25 Mg ha^{-1} during the same period, largely due to the adoption of "Green Revolution" technologies such as the use of high-yielding rice cultivars and intensive application of chemical fertilizers. The atmospheric CO_2 concentration is expected to rise from 380 mmol mol^{-1} currently to between 485 and 1000 mmol mol^{-1} by 2100 [16]. As the consequence of greenhouse effect of many atmospheric gases including CO_2, warming of Earth will occur all the more. In the past 150 years, the global average surface air temperature has increased significantly by 0.05 °C per decade [17]. The predicted changes include the increasein the mean surface temperature of Earth by 1.4–5.8 °C by 2100, the decrease in precipitation in the subtropics and frequent recurrence of extreme events such as flood and drought [16]. At the International Rice Research Institute (IRRI), Manila, Philippines, Peng *et al*. [38] has reported a 1.13°C increase in global nighttime temperature over a period of 25 years (1979–2003). Most of the rice is currently cultivated in regions where temperatures are already above the optimal for growth (28/22°C); therefore, any further increase in mean temperature or episodes of high temperatures during sensitive stages of the crop may adversely affect the growth and yield of rice. According to Baker *et al*. [3], yield decrease was about 7–8% in rice for each 1 °C increase in daytime maximum/nighttime minimum in temperature from 28/21 to 34/27°C. Moreover, the increase in temperature will eliminate the likely benefits of projected rise in atmospheric

(CO_2) on rice plants [22]. The thermal stability of cell membrane is considered to be positively associated with yield performance. Temperature is a major factor for photosynthesis. But, excessive temperatures can result in a decline in foliar photosynthesis and also a decrease in allocation of dry matter to shoots and roots. The adverse effects of high air temperature are not limited to the aboveground portion of rice. As the temperature of floodwater and soil get altered due to high air temperature, the below-ground portion can be equally, if not more affected. This review highlights the global significance of rice, the effects of high temperature due to climate change on growth and development, and yield components of rice and the need for future research studies.

Role of Temperature on Growth and Development of Rice

The physiological response of plants to temperature stress can be (i) tolerance which is due to mechanisms that maintain high metabolic activity under mild stress and reduced activity under severe stress and (ii) avoidance which involves a reduction of metabolic activity, resulting in a dormant state upon exposure to extreme stress. The latter is not relevant to rice production. Critical temperatures define the environmental conditions under which the life cycle of a rice plant can be completed. Generally, rice is adversely affected by high temperature in the lower elevations of the tropics and by lower temperature in the temperate regions. At different times during the life cycle, rice plant is differentially sensitive to temperature stress. Hence, the critically low and high temperatures, normally below 20 °C and above 30°C, vary from one growth stage to another.

Germination

As early as 1933, Livingston and Haasis found out that an incubation of 6 days was required for 90% germination at 25°C, 2 days at 31–36 °C, and an extended period at 0–5 °C. At low temperatures, germination proceeds very slowly and may take a month or longer. Takahashi [42] examined the effects of temperature on germination using rice seeds of variety Ou-no 200, on three aspects such as temperature, time, and germination percentage. In 2 days, about 90–97% germination was attained under incubation at 27–37°C. But, the germination percentage dropped sharply below or above this range. At temperatures between 15 and 37°C, the incubation time for a germination of 90% or higher was about 6 days. No germination occurred at 8 and 45°C. The suppression of germination at supra-optimal temperatures is called thermo-inhibition. The germinating seeds may experience a 25 °C fluctuation in temperature throughout the course of a day, from a minimum of 22°C to a maximum of 47°C over a 12-hour period, under upland (aerobic) conditions. Under irrigated conditions, this fluctuation in temperature in a day will be less.

Seedling growth

A temperature of 22 °C or below is considered subnormal for seedling growth. The seedling growth may be reasonably good up to 35°C, above which it declines sharply. The seedlings will die above 40°C. Nishiyama [33] reported that the critical minimum temperature for shoot elongation ranged from 7 to 16 °C and that for root elongation from 12 to 16°C. The critical minimum for elongation of both shoot and root is, hence, about 10°C.

Leaf emergence

A moderate increase in temperature speeds up leaf emergence, and temperature is a principal environmental determinant of leaf appearance in rice [10]. The phyllochron concept, which is defined as the time interval between the appearances of successive leaf tips [20], is used to predict the appearance of individual leaves, expressed in thermal time, with units of degree days. The leaf appearance rate (LAR) is not constant with time when rice plants are grown at constant temperature [50], suggesting an effect of age.

Tillering

Yoshida [51] reported that higher temperatures increased tiller numbers. At 3–5 weeks after sowing, temperature only slightly affected the tillering rate and the relative growth rate, except at the lowest temperature (22°C) tested. Tiller number per plant determines panicle number which is a key component of grain yield [52]. To some extent, yield potential of a rice cultivar may be characterized by tillering capacity. But, rice plants with more tillers can show a greater inconsistency in mobilizing assimilates and nutrients among tillers, resulting in variations in grain development and yield among tillers [52].

Growth

There are two sequential growth stages: vegetative phase from germination to panicle initiation and reproductive phase from panicle initiation to maturity. In its biphasic growth pattern, the first half phase of vegetative growth of rice precedes the second phase of reproductive growth [52].

Plant height

Kondo and Okamura [21] and Osada *et al.* [35] also reported that the plant height increased with the rise of temperature within the range of 30–35 °C. Kondo and Okamura [21]suggested that the optimum temperature for dry-matter production was lower than or equal to that for stem elongation. In a recent study, Oh-e *et al*. [34] reported that the increase in plant height was steeper under high temperature than under ambient temperature condition.

Tillers and panicles

The optimum temperature for tillering is 25°C at day and 20°C at night [40]. Tillering increases with rising temperature in the range of 15– 33°C. Chaudhary and Ghildyal [5] found that temperatures above 33 °C were unfavorable for tillering. Oh-e et al. [34] observed that the number of tillers per square meter during the early growth period was generally larger under high temperature and the maximum tillering stage was earlier than under normal temperature conditions Panicle differentiation occurs generally at temperatures between 18 and 30°C. During tillering stage, the number of panicles will increase if the air temperature is lower than 20°C [49]. After the active-tillering stage, high temperatures decrease the number of panicles, especially at maturity.

Panicle dry weight

The panicle weight is known to decrease under high temperature [32, 34, 57]. Kim *et al.*[18, 19] reported that the rate of increase in dry matter in the panicle after the heading decreased under high temperature.

Dark respiration

Respiration is considered to be a good indicator of physiological activity [12]. Increased respiration loss could cause the decrease in average grain weight despite the availability of carbohydrates in leaves and culms [27]. Oh-e *et al.* [34] observed that the specific dark respiration for the whole plant was low at transplanting, reached the maximum value at the tillering stage, and gradually decreased thereafter.

Grain filling

High temperatures at flowering and during grain-filling phase reduce yield by causing spikelet sterility and shortening the duration of grain-filling phase [43, 47]. Yoshida and Hara [51] and Oh-e *et al.*[34] observed that the rate of grain growth was faster and the grain-filling period was shorter at higher temperatures. High temperatures above 30°C are generally not favorable for ripening [33]. Morita *et al.*[27] reported that high night temperatures (22/34°C, day/night) were more harmful to grain weight in rice than high day temperatures (34/22°C) and control conditions (22/22°C) at optimum temperature.

Grain quality

Owing to high temperatures during the ripening period, abnormal morphology and coloration occur in rice, probably due to reduced enzymatic activity related to grain filling, respiratory consumption of assimilation products and decreased sink activity [15, 44]. The chalkiness is one of the key factors in determining rice quality and price. In Japan, chalky grains are conventionally classified into different categories such as milky white rice, white-core rice, white-belly rice, white-based rice, and white-back rice [55]. Wakamatsu *et al.* [45] observed that the incidences of white-back kernel and white-based kernel were high when an average temperature during the 20-day period after heading was 27°C or higher. Below that temperature, no such incidence was apparent.

Grain fissuring

Harvesting time should avoid grain fissure formation due to rapid moisture adsorption and improper drying and storage procedures can also cause grain fissuring that can reduce head rice yield (Daniels *et al.,* 1998). From the field and pot experiments to elucidate the effect of meteorological conditions during grain filling on grain fissuring in rice using a total of 13 cultivars, Morito *et al.* [27] found that the percentage of fissured grains was closely related with the temperature and solar radiation conditions during the early stage of grain filling.

Yield

As early as, Matsu. *et al* ., [25] 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. However, Murata [33] 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 in Kyushu, southern Japan.

Symptoms of High-Temperature Injury in Rice

Ultra-structural changes

Under high-temperature stress conditions, there is a tendency for reduced cell size, closure of stomata and curtailed water loss (usually not observed in high light conditions, until there has been a temperature more than 35°C), increased stomata and trichomatous densities, and greater xylem vessel numbers of both root and shoot [4]. High-temperature stress led to different responses; thermo-resistant line 996 showed tightly arranged mesophyll cells in flag leaves, fully developed vascular bundles, and some closed stomata, whereas the line 4628 suffered from injury because of undeveloped vascular bundles, loosely arranged mesophyll cells, and opened stomata.

Phenological changes
It is unknown whether damaging effects of heat episodes occurring at different developmental stages are cumulative [46]. All vegetative and reproductive stages are affected by heat stress to some extent: high day temperature can damage leaf gas exchange properties during the vegetative stage and even a short period of heat stress can cause significant increases in the abortion of floral buds and opened flowers during the reproductive stage [11].
Physiological changes
Water
The grains of rice plants grown at 30 °C had free water for shorter period (22 days after flowering) than those grown at 20 °C (28 days after flowering; [9]. Thereafter, they found grains having only loosely bound water and bound water.
Chlorophyll fluorescence
Yamada *et al.* [48] suggested that the physiological parameters such as chlorophyll fluorescence, the ratio of variable fluorescence to maximum fluorescence (F_v/F_m), and the base fluorescence (F_0) correlate with heat tolerance. The maximal quantum yield of PSII photochemistry (F_v/F_m) is an important parameter for the PSII activity and any decrease in F_v/F_m indicates the loss of PSII activity.
High-Temperature Injury and Rice Crop Production
As the most common tropical food cereal, rice is generally considered to be adapted to high-temperature regions, nevertheless, optimum temperatures exist for each growth stage, and that temperatures exceeding the optimum often occur under field conditions [36].
Growth-stage-dependent responses
The leaf weight increases up to flowering and then decreases due to drying and death of lower leaves. Likewise, the dry weight of leaf sheath and culm increases up to flowering, followed by a decline due to translocation of accumulated plant reserves to panicles. The vegetative phase is divided into two sub phases: (i) the active-vegetative phase that lasts to maximum tillering and is accompanied by a rapid increase in plant height and tiller number and dry-matter production and (ii) vegetative-lag phase continues up to panicle initiation. During the vegetative-lag phase, maximum tillering, internode elongation, and panicle initiation occur almost simultaneously in cultivars of 105–120 days duration and successively later in cultivars of more than 140 days duration. Temperatures above 35 °C cause different types of heat injury to rice crop, depending on the cultivar and growth stage [54]. There are reports that the total dry weight of cv. IR747B2-6 at 35/25 °C was only one-sixth of that at 30/25 °C. In 2 days at 45/25 °C, leaves became discolored and desiccated, gradually dried from the tip to the base, and died 9 days later [52].
Seedling stage
The optimum temperature for germination is between 30 and 35 °C, and under suitable conditions, the seed absorbs water to about 25% of its dry weight. The first indication of germination is detectable after about 2 days. When the growing tips of vegetative parts are under floodwater or soil, its temperature greatly affects the growth and development. High-temperature stress can do harm to germination and seedling emergence and even lead to death if it takes place during the seedling stage. The long-term effects of high-temperature stress may include delayed germination or loss of vigor, leading to reduced emergence and seedling establishment.
Flowering
The reproductive growth generally begins just before or after the maximum tillering stage and is characterized by culm elongation, emergence of the flag leaf, booting, and heading and filling of the spikelets [53]. The panicle, composed of a base axis, primary and secondary branches, rudimentary glumes, and spikelets, extends upward inside the flag leaf sheath, and booting (swelling of the flag leaf sheath) occurs in the later part of panicle development, followed by emergence of the panicle out of the flag sheath (heading).
Yield and its components
The number of panicles is closely associated with grain yield, but there is often a negative correlation between the number of panicles per unit land area and spikelets per panicle and between spikelets per unit land area and filled-grain percentage or 1000-grain weight [54]. High temperature (40/33/37 °C, daytime dry bulb air temperature/nighttime dry bulb air temperature/paddy water temperatures) during stem elongation led to death of rice plants while CO_2 enrichment (660 mmol CO_2 mol^1 air) helped plants to survive, but with sterile panicles [5]. As a result of high temperature, the extent of sterility can vary from a few empty glumes to the entire panicle having unfilled grains. Temperatures below 20°C or above 35°C and radiation lower than 200 cal cm^2 day^1 at anthesis can result in up to 40–60% sterility. Seed set and panicle weight of rice plants grown at higher temperatures (ambient 4°C) are significantly reduced while green leaf area increased, relative to those plants grown at ambient temperatures [24].

Generally, the rice cultivars with high yield potential have grain weights in the range of 20–30 g and grain weight generally follows the order of maturity within a panicle, the first maturing grain being the heaviest. High temperature can increase the grain growth rate, but decrease the grain-filling period [3]. The rice yield in the temperate or high altitude subtropical or tropical environments shows plasticity in the yield components and there are strong compensation mechanisms, particularly, for panicle and spikelet number in crops under tropical conditions.

Grain quality

Grain quality is generally classified into four components: milling efficiency, grain shape and appearance, cooking and edibility characteristics, and nutritional quality. In most breeding programs, the major grain quality considerations are milling efficiency (head rice yield), shape and appearance (grain length before and after cooking, grain width and chalkiness), cooking and edibility characteristics (amylase content of the endosperm, gelatinization temperature and aroma), and nutritional quality (protein, oil, and micronutrient content) [45].

Mechanism of high heat injury

Environmental factors are not always at optimal conditions and may reach a level which represents stress for plants. Stress can cause variable effects at all functional levels of plants. When plants are exposed to stresses, there are decreases in activities and energy for growth and development. Crop losses can occur eventually due to stresses.

Photosynthesis

Photosynthesis is sensitive to high-temperature stress, and maintenance of high photosynthetic capacity is critical for tolerance. The temperature optimum for photosynthesis in rice is broad, presumably because rice plants have adapted to a relatively wide range of thermal environments. In rice, there is little temperature effect on leaf photosynthesis from 20 to 40 ^{o}C (Egeh *et al.,* 1992). Single leaves of rice show a cooperative enhancement of photosynthetic rate with elevated [CO_2] and temperature during tillering, relative to the elevated [CO_2] [24]. At flowering stage, photosynthetic stimulation by elevated [CO_2] appeared to be accompanied by a reduction in ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco [EC 4.1.1.39]) activity and/or concentration as evidenced by the reduction in the assimilation at a standard internal [CO_2] (Ci). High temperature can reduce photosynthetic rate by 40–60% at mid-ripening, leading to more rapid senescence of the flag leaf [34].

The light-saturated photosynthetic rates of leaves are highly correlated with atmospheric [CO_2], and temperature dependence of photosynthesis varies with the growing temperature, even within a genotype [34]. With changes in growth temperature, rice may show considerable phenotypic plasticity in its photosynthetic characteristics. Temperature dependence of photosynthesis is sensitive to the [CO_2] and the optimal temperature increases with [CO_2]. Lin *et al.* [24] showed a cooperative enhancement of photosynthetic rate with temperature under elevated [CO_2] during tillering stage relative to the elevated [CO_2] condition alone. How-ever, after flowering, the degree of photosynthetic stimulation by elevated [CO_2] was reduced under high temperature (ambient þ4 C). This increasing insensitivity to [CO_2] under high temperature was attributed to the reduction in Rubisco activity. The acclimation of photosynthesis to increasing temperatures may occur at the whole-leaf level or in isolated chloroplasts. The physiological acclimation may result in increases in both the heat tolerance and the temperature optimum for net CO_2 uptake of leaves.

Respiration

Respiration is typically partitioned into growth respiration (the functional components of construction) and maintenance respiration (of maintenance and ion uptake)[2,23]. Growth respiration is temperature dependent, only because it follows growth rate. But, the growth efficiency, which depends on the ratio of respiration and growth rate, may be independent of temperature. Increased respiration can lead to the production of reactive oxygen species, which can decrease membrane thermal stability. Maintenance respiration is mainly associated with turnover of proteins and lipids and maintenance of ion concentration gradients across membranes [39]. Any increase in respiration in response to climate warming is of serious concern, as respiratory processes could consume a larger portion of total photosynthates [37]. High nighttime temperatures are generally considered to be disadvantageous because they can stimulate respiration [56]. Mohammed and Tarpley [26] showed that there were no differences among the rice plants grown under high night temperature (32^{o}C) and ambient night temperature (27^{o}C) for leaf respiration rates at boot or mid-dough stage.

Heat shock proteins

In general, Hsps are induced by heat stress at any stage of development. Under maximum heat stress conditions, Hsp70 and Hsp90 mRNAs can increase 10-fold and low molecular weight Hsp increase as much as 200-fold. In rice, heat-responsive gene profiling differed largely from those under cold/drought/salt stresses [14]. In the cells of callus derived from rice seed embryos, heat shock depresses normal protein synthesis, but enhances the synthesis of specific proteins. Depending on whether the temperature increase is rapid or gradual, differences are observed in the production of Hsps.

Membrane injury

The cellular membranes, which regulate the flow of materials between cells and the environment as well as their internal compartments, are the critical sites of high-temperature stress. The membranes are the first structures involved in the perception and transmission of external stress signals. Adverse effects of temperature stress on the membranes include the disruption of cellular activity or death. Injury to membranes from a sudden heat stress event may result either from denaturation of the membrane proteins or from melting of membrane lipids, which leads to membrane rupture and loss of cellular content, and is measured by ion leakage. The membrane lipids are highly susceptible to changes in temperature and consequently changes in membrane fluidity, permeability, and cellular metabolic functions. Lipid saturation level typically increases, whereas unsaturated lipids decrease with increasing temperature. High temperature fluidizes by melting the lipid bi-layer, increasing membrane permeability, and increasing leakage of ions and other cellular compounds from the cell. Modifications in membrane structure and composition play a key role in plant adaptation to high-temperature stress. In fact, maintaining proper membrane fluidity is essential for temperature stress tolerance.

Pollen germination

Temperature stress reduces the percentage of anthers dehiscing at the time of flowering [41]. Pollination is sensitive to temperature: high temperatures at the time of flowering inhibit the swelling of pollen grains [25], whereas low temperatures at the booting stage impede pollen growth [41]. High (>35 ^oC) and low (<20 ^oC) temperatures can result in poor pollination and loss of yield [13].

Mitigation and Adaptation to High-Temperature Stress

Mitigation

IPCC [16] defines mitigation as the technological change or substitution that reduces resource inputs and emissions per unit of output. Concerns are more placed on the emission of greenhouse gases. Rice cultivation will not only suffer from the adverse effects of climate change but also contributes to climate change. The submerged rice fields are an important source of greenhouse gas methane. The mitigation technologies should aim at reducing the emission of methane and other greenhouse gases. High temperatures due to climate change are resultant events due to many interlinked activities. Hence, the options for mitigation can encompass many activities which are aimed at reducing the resource inputs and emissions per unit of output. Some of the suggested mitigation options related to rice cultivation are presented below:

- Improved crop and land management to increase soil carbon storage.
- Improved rice cultivation techniques to reduce CH_4 emissions.
- Improved nitrogen fertilizer application techniques to reduce N_2O emissions from rice fields.
- Use of rice straw for replacing fossil fuel use and generation of energy.
- Restoration of degraded lands for rice cultivation.
- Improved energy efficiency.

ADAPTATION

- Developing tolerant rice cultivars for high-temperature stress
- Adopting a late or early maturing cultivar and shifting the crop season
- Changing planting dates
- Pretreatment of rice seedlings
- Application of chemical substances
- Developing high-temperature-tolerant transgenic rice
- Conserving soil moisture
- Modification of microclimate
- Establishment of soil covers
- Land-use change

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CITATION OF THIS ARTICLE

Akhila Nand Dubey, Sudhanshu Verma, Suhana Puri Goswami, Anoop Kumar Devedee. Effect of Temperature on Different Growth Stages and Physiological Process of Rice crop- As a Review. Bull. Env. Pharmacol. Life Sci., Vol 7 [11] October 2018: 162-169