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Physiological Responses of Plants under High **Temperature Stress**

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Supriva Debnath^{1*}, Mandakranta **Chakraborty² and Rohit Kumar** Kumawat¹

¹College of Agriculture, Jawaharlal Nehru Krishi Viswavidyalaya, Jabalpur, Madhya Pradesh (482 004), India ²College of Agriculture, CSK HPKV, Palampur, Himachal Pradesh (176 062), India



Corresponding Author

Supriya Debnath e-mail: supriyadebnath05@gmail.com

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E-mail: bioticapublications@gmail.com



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Abstract

igh temperature has become a global concern, which seriously affects the growth and production of crops. Thus, the physiological response of heat stress in plants has been a focus of research to protect food production and ensure crop safety. However, the plant response to HS involves complex physiological traits (photosynthesis, cell membrane thermostability, oxidative damage, and others). In addition, the production of heat stress response elements during particular physiological periods of the plant is described. Here we attempt to summarize, the production of heat stress response elements during physiological periods of the plant also discussed the future prospects concerning of the heat stress response in plants.

Introduction

eing a sessile organism, plants cannot move to favorable environments upon encountering abiotic or biotic stresses; consequently, plant growth, development, and productivity are markedly affected. High temperature is an important stress and global warming has accelerated the increase in air temperature in recent decades. The global air temperature is predicted to rise by 0.2 °C per decade, which will lead to temperatures 1.8-4.0 °C higher than the current level by 2100. Therefore, the mechanisms by which plants respond to high temperature are of great interest. Plants exposed to high temperature (heat stress, HS) suffer from adverse effects. To cope with such conditions, plants have evolved some mechanisms to respond to HS. For example, several basic physiological processes of plants including photosynthesis, respiration, and water metabolism respond to HS. Here, we focus on the physiological responses of the plant when exposed to HS.

Physiological Responses to HS

ifferent physiological processes such as photosynthesis, respiration, transpiration, membrane thermostability, and stomatal conductance are adversely affected by HS. Some common effects of HS on plant physiological responses, growth and development, and yield are shown in Figure 1.

Photosynthesis

igh temperature has a greater influence on the photosynthetic capacity of plants especially of C, plants than C_{A} plants. Under heat stress condition, disruption of thylakoid membranes occurs, thereby inhibiting the activities of membrane associated electron carriers and enzymes, reducing the rate of photosynthesis. Specifically, photosystem II (PSII) activity is greatly reduced or even stops under HS because PSII complex is the most heat-intolerant. Temperatures higher than 35 °C significantly decrease the activity of ribulose 1,5-bisphosphate carboxylase/ oxygenase (Rubisco), thereby limiting photosynthesis (Crafts-Brandner and Law, 2000).

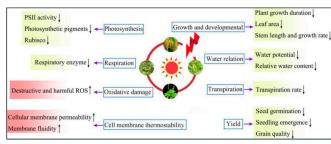


Figure 1: Effects of heat stress on plant physiological responses. Upward-pointing arrows and Downward-pointing arrows indicates activated/ up-regulated and deactivated/ downregulated physiological indices respectively

Respiration

s temperature increases, the rate of dark respiration increases, thereby using more carbohydrates for growth and maintenance. Elevated temperature will increase the extent of oxygenase activity because the solubility of O, increases in relation to CO, as temperature increases.

Stomatal Conductance

igh temperature has detrimental impact on stomatal conductance. Under high temperature stress condition, stomatal apertures open to allow evaporative cooling through the release of water vapor. When stomatal pores open, the supply of CO_2 available for the photosynthetic enzymes is increased.

Growth and Development

n most of the determinate annual crop species, increases in temperature, shortens the duration of growth. This results in less time for photosynthetic carbon assimilation and biomass accumulation before the start of reproductive growth. Increasing temperature, up to about 25 °C for wheat and 35 °C for soybean, generally increases vegetative growth rates. The major impacts of heat stress are reduced germination percentage, plant emergence, abnormal seedlings, poor seedling vigor, reduced radicle and plumule growth of geminated seedlings. At HT (45 °C) the germination rate of wheat was strictly prohibited and caused cell death for which seedling establishment rate was also reduced. Under HT condition, Plant height, number of tillers and total biomass were reduced in rice cultivar. High temperature leads to reduction in relative water content in leaf tissue which decreases the cell size and ultimately the growth is reduced. High temperature may alter the total phenological duration by reducing the life period.

Flower Initiation

During reproduction, a short period of heat stress can cause significant decrease in floral buds and flowers abortion although great variations in sensitivity within and among plant species and variety exist. Even heat spell at reproductive developmental stages plant may produces no flowers or flowers may not produce fruit or seed. A combination of shortened daylength (photoperiod) and cooler temperatures is necessary to induce flowering in many autumns season crops. Flowers may abort before producing seed due to the sensitivity of pollen and fertilization to increased high temperature.

Pollen Production and Viability

Pollen production and pollen viability are very sensitive to slight increases in temperature above optimum. Daytime temperature > 34 °C significantly reduces pollen production and viability of peanut (*Arachis hypogea*), a warmseason crop. Cool-season plants, like wheat or some cultivars of dry bean (*Phaseolus* spp.), require cooler temperatures than peanut. High night temperatures (32 °C) increase in spikelet sterility in rice which was resulted from decreased pollen germination. High temperature aborts floral buds, flowers and pods, loss of pollen viability and fertility ultimately leading to reduced seed set, size and yield (Devasirvatham *et al.*, 2015). High temperature stress resulted in abscission and abortion of flowers, young pods and developing seeds, resulting in lower seed numbers in soybean.

Transpiration and WUE

Increased ambient temperature would increase transpiration because evaporation from the leaf increases with increased temperature; thus, higher temperature would lead to increased water use by increasing evapotranspiration. In contrast, water use efficiency (WUE), will decrease at elevated temperatures due to increased transpiration. Decreased WUE will be a problem in areas that are already limited in water resources and will increase the amount of water required for irrigation.

Cell Membrane Thermostability

f plants are exposed to HS, membrane dysfunction is the main physiological consequence. High temperature can cause a significant alteration in membrane composition and hence its permeability characteristics. Under extreme HS, the kinetic energy increased and thus movement of biomolecules across membranes loosens the chemical bonds, leading to disintegration of membrane lipids and increasing membrane fluidity. HS increases cellular membrane permeability and the loss of cellular electrolytes which inhibits cellular functions and decreased thermotolerance. In addition, the reactive oxygen species (ROS) accumulation caused by HS leads to membrane



damage, decreasing thermotolerance. Hence, cell membrane thermostability playscrucial role in conferring tolerance to HS in plants.

Oxidative Damage

etabolic pathways of plants are depended upon enzymes which are sensitive to high temperature stress. It has been revealed that under exposure to heat stress leading to uncouple of enzymes and metabolic pathways which causes the accumulation of unwanted and harmful ROS most commonly singlet oxygen (¹O₂), superoxide radical (O₂⁻), hydrogen peroxide (H₂O₂) and hydroxyl radical (OH⁻) generating oxidative stress. The reaction centers of PSI and PSII in chloroplasts are the major sites of ROS generation though ROS are also generated in other organelles viz. peroxisomes and mitochondria (Figure 2). ROS (e.g., O₂, H₂O₂) induce oxidative stress by altering membrane properties, degradation of proteins, and enzymes in activation. Thermal stress can induce oxidative stress through peroxidation of membrane lipids and disruption of cell membrane stability by protein denaturation. Plants increase their thermotolerance by recruiting the antioxidant enzymes superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR) and peroxidase (POX).

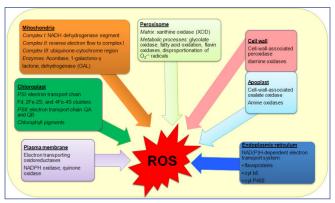


Figure 2: Sites of production of Reactive Oxygen Species in plants **Yield**

ncreases in temperatures 1-2 °C than the optimum result in shorter grain filling periods and negatively affect yield components of cereal. Higher temperatures affect the grain yield mostly through affecting phenological development processes. Heat induced yield reduction was documented in many cultivated crops including cereals (*e.g.*, rice, wheat, barley, sorghum, maize), pulse (*e.g.*, chickpea, cowpea), oil yielding crops (mustard, canola) and so on. The sensitive crop varieties are more severely affected by heat stress relative to tolerant varieties. Elevated temperature affects the performance and crop quality characteristics. Grain quality characteristics in barley significantly changed under heat stress.

Conclusion and Perspectives

igh temperature stress has become a major concern for crop production worldwide because it greatly affects the growth, development, productivity and quality of plants. The present rate of emission of greenhouse gases from different sources is believed responsible for a gradual increase in the world's ambient temperature, and is resulting in global warming. Therefore, plant responses and adaptation to elevated temperatures, and the mechanisms underlying the development of heat-tolerance, need to be better understood for important agricultural crops. Though, plant responses to HT also vary across within species and at different developmental stages.

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