Journal of Pharmacognosy and Phytochemistry 2019; 8(5): 1732-1737

Journal of Pharmacognosy and Phytochemistry
Available online at www.phytojournal.com

E-ISSN: 2278-4136
P-ISSN: 2349-8234
JPP 2019; 8(5): 1732-1737
Received: 28-07-2019
Accepted: 30-08-2019

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Mechanisms of heat stress tolerance in plants: A physiological approach

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Abstract
High temperature (HT) stress is a major environmental stress that limits plant growth, metabolism, and productivity worldwide. Plant responses to HT vary with the degree and duration of HT and the plant type. HT is now a major concern for crop production and approaches for sustaining high yields of crop plants under HT stress are important agricultural goals. Plants possess a number of adaptive, avoidance, or acclimation mechanisms to cope with HT situations. Plant survival under HT stress depends on the ability to perceive the HT stimulus, generate and transmit the signal, and initiate appropriate physiological and biochemical changes. HT-induced gene expression and metabolite synthesis also substantially improve tolerance. The physiological responses to heat stress are active research areas. This article reviews the recent findings on responses, adaptation, and tolerance to HT in plants.

Keywords: Abiotic stress, climate change, high temperature, heat shock proteins, oxidative stress

1. Introduction

Among the ever-changing components of the environment, the constantly rising ambient temperature is considered one of the most detrimental stresses. 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 [1]. This prediction is creating apprehension among scientists, as heat stress has known effects on the life processes of organisms, acting directly or through the modification of surrounding environmental components. Plants, in particular, as sessile organisms, cannot move to more favorable environments; consequently, plant growth and developmental processes are substantially affected, often lethally, by high temperature (HT) stress [2, 3]. Heat stress causes multifarious, and often adverse, alterations in plant growth, development, physiological processes, and yield [4, 5] (Figure 1). One of the major consequences of HT stress is the excess generation of reactive oxygen species (ROS), which leads to oxidative stress [4, 5]. Plants continuously struggle for survival under various environmental stress conditions including HT. A plant is able, to some extent, to tolerate heat stress by physical changes within the plant body and frequently by creating signals for changing metabolism. Plants alter their metabolism in various ways in response to HT, particularly by producing compatible solutes that are able to organize proteins and cellular structures, maintain cell turgor by osmotic adjustment, and modify the antioxidant system to re-establish the cellular redox balance and homeostasis [6-8]. At the molecular level, heat stress causes alterations in expression of genes involved in direct protection from HT stress [9, 10]. These include genes responsible for the expression of osmoprotectants, detoxifying enzymes, transporters, and regulatory proteins [11, 12]. In conditions such as HT, modification of physiological and biochemical processes by gene expression changes gradually leads to the development of heat tolerance in the form of acclimation, or in the ideal case, to adaptation [13, 14]. In recent times, exogenous applications of protectants in the form of osmoprotectants (proline, Pro; glycine betaine, GB; trehalose, Tre, *etc.*), phytohormones (abscisic acid, ABA; gibberellic acids, GA; jasmonic acids, JA; brassinosterioids, BR;salicylic acid, SA; *etc.*), signaling molecules (e.g., nitric oxide, NO), polyamines (putrescine, Put; spermidine, Spd and spermine, Spm), trace elements (selenium, Se; silicon, Si; *etc.*) and nutrients (nitrogen, N; phosphorus, P; potassium, K, calcium, Ca; *etc.*) have been found effective in mitigating HT stress-induced damage in plants [15-21]. Development of new crop cultivars tolerant to HT is a major challenge for plant scientists [13, 22]. Depending upon the extremity and duration, and also depending upon the plant types and other environmental factors in the surroundings, plants show dynamic responses to HT, but identification and confirmation of the traits that confer tolerance to HT still remain elusive [23, 24]. Plant scientists involved in research on HT stress are endeavoring to discover the plant responses that lead to heat tolerance and they are also trying to investigate how plants can be managed in HT environments.

2. Plant Response to Heat Stress

Plant responses to HT vary with the degree of temperature, duration and plant type. At extreme HT, cellular damage or cell death may occur within minutes, which may lead to a catastrophic collapse of cellular organization [28]. Heat stress affects all aspects of plant processes like germination, growth, development, reproduction and yield [5, 29-31]. Heat stress differentially affects the stability of various proteins, membranes, RNA species and cytoskeleton structures, and alters the efficiency of enzymatic reactions in the cell for which the major physiological processes obstacle and creates metabolic imbalance [32-35]. Some common effects of heat stress have been summarized in Table 1.

Table 1: Effects of high temperature stress in different crop species.

Crops	Heat treatment	Growth stage	Major effects	References
Rice (*Oryza sativa*)	Above 33 °C, 10 days	Heading stage	Reduced the rates of pollen and spikelet fertility.	[37]
Wheat (*Triticum aestivum*)	37/28 °C (day/night), 20 days	Grain filling and maturity stage	Shortened duration of grain filling and maturity, decreases in kernel weight and yield.	[38]
Wheat (*Triticum aestivum*)	30/25 °C day/night	From 60 DAS to maturity stage	Reduced leaf size, shortened period for days to booting, heading, anthesis, and maturity, drastic reduction of number of grains/spike and smaller grain size and reduced yield.	[39]
Maize (*Zea mays*)	35/27 °C (day/night), 14 days	Reproductive stage	Reduced ear expansion, particularly suppression of cob extensibility by impairing hemicellulose and cellulose synthesis through reduction of photosynthate supply.	[42]
Soybean (*Glycine max*)	38/28 °C (day/night), 14 days	Flowering stage	Decreased the leaf Pn and stomatal conductance (*gs*), increased thicknesses of the palisade and spongy layers, damaged plasma membrane, chloroplast membrane, and thylakoid membranes, distorted mitochondrial membranes, cristae and matrix.	[44]

2.1. Growth

Among the growth stages of plant the germination is affected first of all. Heat stress exerts negative impacts on various crops during seed germination though the ranges of temperatures vary largely on crop species [49, 50]. Reduced germination percentage, plant emergence, abnormal seedlings, poor seedling vigor, reduced radicle and plumule growth of geminated seedlings are major impacts caused by heat stress documented in various cultivated plant species [50-52]. Inhibition of seed germination is also well documented in HT which often occurs through induction of ABA [53]. At very HT (45 °C) the rate of germination of wheat was strictly prohibited and caused cell death and embryos for which seedling establishment rate was also reduced [54]. Plant height, number of tillers and total biomass were reduced in rice cultivar in response to HT [55].

High temperature causes loss of cell water content for which the cell size and ultimately the growth is reduced [24, 56]. Reduction in net assimilation rate (NAR) is also another reason for reduced relative growth rate (RGR) under HT which was confirmed in maize and millet [57] and sugarcane [58]. The morphological symptoms of heat stress include scorching and sunburns of leaves and twigs, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage [24]. Damage to leaf-tip and margins, and rolling and drying of leaves, necrosis, was observed in sugarcane due to HT stress [59]. In common bean (*Phaseolus vulgaris*) morphophysiological characteristics such as phenology, partitioning, plant-water relations, and shoot growth and extension are seriously hampered by heat stress [60]. In some plant species growth at HTs (28/29 °C) cause noteworthy elongated stems and entended leaves (hyponasty) and diminish in total biomass [61, 62]. Reduced number of tillers with promoted shoot elongation was observed in wheat plant under heat stress [50]. In wheat green leaf area and productive tillers/plant were drastically reduced under HT (30/25 °C, day/night) [39]. High temperatures may alter the total phenological duration by reducing the life period. Increases in temperatures 1–2 °C than the optimum result in shorter grain filling periods and negatively affect yield components of cereal [22, 63]. In *T. aestivum* HT (28 °C to 30 °C) reduced the germination period, days to anthesis booting, maturity that is ultimate the total growth duration [64]. At extreme heat stress plants can show programmed cell death in specific cells or tissues may occur within minutes or even seconds due to denaturation or aggregation of proteins, on the other hand moderately HTs for extended period cause gradual death; both types of injuries or death can lead to the shedding of leaves, abortion of flower and fruit, or even death of the entire plant [14, 24].

2.2. Photosynthesis

Photosynthesis is one of the most heat sensitive physiological processes in plants [65]. High temperature has a greater influence on the photosynthetic capacity of plants especially of C3 plants than C4 plants [66]. In chloroplast, carbon metabolism of the stroma and photochemical reactions in thylakoid lamellae are considered as the primary sites of injury at HTs [67, 68]. Thylakoid membrane is highly susceptible to HT. Major alterations occur in chloroplasts like altered structural organization of thylakoids, loss of grana stacking and swelling of grana under heat stress [24, 56]. Again, the photosystem II (PSII) activity is greatly reduced or even stops under HTs [69]. Heat shock reduces the amount of photosynthetic pigments [68].

The ability of plant to sustain leaf gas exchange and CO2 assimilation rates under heat stress is directly correlated with heat tolerance [66, 70]. Heat markedly affects the leaf water status, leaf stomatal conductance (*gs*) and intercellular CO2 concentration [71]. Closure of stomata under HT is another reason for impaired photosynthesis that affects the intercellular CO2 [56]. The decline in chl pigment also is a result of lipid peroxidation of chloroplast and thylakoid membranes as observed in sorghum due to heat stress (40/30 °C, day/night) [40]. Photosystem II photochemistry (Fv/Fm ratio) and *gs* were also reduced under the same stress condition. All these events significantly decreased the photosynthesis compared with OT in sorghum [40]. In soybean, heat stress (38/28 °C) significantly decreased total chl content (18%), chl *a* content (7%), chl *a*/*b* ratio (3%), Fv/Fm ratio

(5%), Pn (20%) and *gs* (16%). As a result decreased in sucrose content (9%) and increased reducing sugar content (47%) and leaf soluble sugars content (36%) were observed [44]. In rice plants, HT (33 °C, 5 days) decreased the photosynthetic rate by 16% in the variety Shuanggui 1 and 15% in T219 [37]. Greer and Weedon [72] observed that average rates of photosynthesis of *Vitis vinifera* leaves decreased by 60% with increasing temperature from 25 to 45 °C. This reduction in photosynthesis was attributed to 15%–30% stomatal closure.

Some other reasons believed to hamper photosynthesis under heat stress are reduction of soluble proteins, Rubisco binding proteins (RBP), large-subunits (LS), and small-subunits (SS) of Rubisco in darkness, and increases of those in light [73]. High temperature also greatly affects starch and sucrose synthesis, by reduced activity of sucrose phosphate synthase, ADP-glucose pyrophosphorylase, and invertase [24, 74]. Heat imposes negative impacts on leaf of plant like reduced leaf water potential, reduced leaf area and pre-mature leaf senescence which have negative impacts on total photosynthesis performance of plant [71, 75]. Under prolonged heat stress depletion of carbohydrate reserves and plant starvation are also observed [74].

2.3. Reproductive Development

Although all plant tissues are susceptible to heat stress at almost all the gowth and developmental stages, the reproductive tissues are the most sensitive, and a few degrees elevation in temperature during flowering time can result in the loss of entire grain crop cycles [30]. 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 exists [76]. Even heat spell at reproductive developmental stages plant may produces no flowers or flowers may not produce fruit or seed [77, 78]. The reasons for increasing sterility under abiotic stress conditions including the HT are impaired meiosis in both male and female organs, impaired pollen germination and pollen tube growth, reduced ovule viability, anomaly in stigmatic and style positions, reduced number of pollen grains retained by the stigma, disturbed fertilization processes, obstacle in growth of the endosperm, proembryo and unfertilized embryo [79].

HT treatment (>33 °C) at heading stage significantly reduced anther dehiscence and pollen fertility rate, leading to reduction in the number of pollens on the stigma which were the causes of reduced fertilization and subsequent spikelet fertility and sterile seed in rice [37, 80] where the sensitive varieties were more suseptable to this occurrence compared to the tolerant varieties [37]. High night temperatures (32 °C) increase in spikelet sterility (by 61% compared to control) in rice which was resulted from decreased pollen germination (36%) of rice [41]. High temperature often causes excessive ethylene (Eth) production and leads to male sterility of rice pollens. The Eth is hypothesized to inhibit the key enzymes in sugar–starch metabolism which weaken sink strength and restrict grain filling and ultimately produce sterile grain. Due to late sowing-induced heat stress the ear length, number of spikelet main stem−1, no. of fertile floret main stem−1 were reduced significantly in wheat plant those resulted in reduced grain yield [81]. Edreira and Otegui [47] observed that heat stress at flowering periods, more specifically at pre-silking and silking stages resulted higher yield reduction relative to the heat stress at grain filling stage of maize. High temperature stress resulted in abscission and abortion of flowers, young pods and developing seeds, resulting in lower seed numbers in soybean [82]. High temperatures at flowering are known to decrease pollen viability in soybean [44].

2.4. Yield

Elevated temperatures are raising apprehension regarding crop productivity and food security [62]. Its affect is so terrible that even a small (1.5 °C) increase in temperature have significant negative effects on crop yields [83]. 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 [47, 78, 80, 82, 84, 85].

It was demonstrated that increase of the seasonal average temperature 1 °C decreased the grain yield of cereals by 4.1% to 10.0% [86]. The sensitive crop varieties are more severely affected by heat stress relative to tolerant varieties. At heat stress of 35–40 °C the 1000-grain weight was reduced by 7.0%–7.9% in sensitive Shuanggui 1 and 3.4%–4.4% in tolerant Huanghuazhan variety of rice. The higher yield reduction was also observed in heat-sensitive rice cultivar Shuanggui 1 (35.3% to 39.5%) compared to heat tolerant cultivar Huanghuazhan (21.7% to 24.5%) [80]. High night temperature (32 °C) decreased grain length (2%), width (2%), and weight in *O. sativa* and increased spikelet sterility (61%). It also increased grain nitrogen (N) concentration (44%) which was inversely related to grain weight. All of these factors contributed to reduced yield (90%) [41]. Heat stress modifies the early dough and maturity stage shorten the kernel desiccation period and cause grain yield loss in wheat [48]. Heat also reduces the single kernel weight and it is the major contributor to the yield loss [87]. Compared to OT late sowing mediated heat stress (28–30 °C) caused significant reduction of yield in different wheat varieties, viz. 70% reduction in “Sourav”, 58% in “Pradip”, 73% in “Sufi”, 55% in “Shatabdi” and 53% in “Bijoy” [64]. In sorghum, due to heat stress, filled seed weight and seed size were reduced by 53% and 51% respectively, which ultimately reduced the yield [40]. In canola (*Brassica* spp.), seed yield on the main stem was reduced by 89%, but all branches contributed to overall yield loss of 52% at HT of over 30 °C. The cause of this yield decline was due to heat induced infertile pods, reduced seed weight and seeds per pod [88].

Loss of productivity in heat stress is chiefly related to decreased assimilatory capacity [89] which is due to reduced photosynthesis by altered membrane stability [22] and enhanced maintenance respiration costs [90], reduction in radiation use efficiency (RUE, biomass production per unit of light intercepted by the canopy). These occurrences were documented in wheat [91] and maize [92]. High temperature (33–40 °C) in maize negatively affected light capture, RUE, biomass and gain yield, harvest index although heat at the flowering stage resulted higher yield reduction than at grain filling period [47]. Elevated temperature affects the performance and crop quality characteristics. Grain quality characteristics in barley significantly changed under heat stress. In barley grain several proteinogenic amino acids concentrations and maltose content increased, where the concentrations of total non-structural carbohydrates, starch, fructose and raffinose, lipids and aluminum were reduced [93]. Damages in pod quality parameters such as fibre content and break down of the Ca pectate were foundin okra (*Abelmoschus esculentus*) at HT stress [46].

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