Increasing Productivity of Wheat in Rajasthan Under Heat Stress Condition

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Abstract

Wheat is major cereal crop for fulfilling the calories demands of growing population. Alterations in the worldwide climate are predicted to have critical sentence forcrop production. Abiotic stresses such as heat and drought are major abiotic stresses restraining crop production. Heat stress reduces wheat growth by upsetting various physiological and biochemical processes and the developmental stage of the plant is critical in demonstrating the vulnerability of various species and cultivars subjected to high temperature. Heat stress did not affect the protein content but there is strong correlation between leaf nitrogen content and grain protein content. Induction of HSPs seems to be the universal response and adaptation to temperature stress. The synthesis of HSPs is believed to play significant role either in preventing or minimizing the adverse effects of high temperature both at molecular and cellular levels. Wheat has the tendency to adopt diverse types of responses to temperature stress as well as a heat shock by developing thermo-tolerance for the enhancement of the grain quality and yield.

Introduction

Majority of the world's population depends upon wheat as cereal food which belongs to family Poaceae[1]. It has been described as the 'King of cereals' because of its cultivation on huge area, its potential to give high productivity and the prominent position in international food grain trade. The majority of the cultivated wheat varieties belong to three main species of the genus Triticum. These are the hexaploid, Triticum aestivum L. (bread wheat), and the tetraploid, T. durum, T. dicoccum and T. monococcum [2]. It has good nutrition profile with 12.1% protein, 1.8% lipids, 1.8% ash, 2.0% reducing sugars, 6.7% pentosans, 59.2% starch, 70% total carbohydrates and provides 314 K cal/100 g of food. It is also a good source of minerals and vitamins viz., calcium (37 mg/100 g), iron (4.1 mg/100 g), thiamine (0.45 mg/100 g), riboflavin (0.13 mg/100 g) and nicotinic acid (5.4 mg/100 mg) [3].

Wheat Demands

The forecasts demand for 2020 to fulfill the need of growing world population varies between 840 and 1050 million ton [4,5]. The Green Revolution enabled food production in developing countries to keep pace with population growth [6]. Enhancement in crop yield has slowed since 1990s [7,8]. However, increased crop yield is the need of the hour to meet the feeding demand of the world in the 21st century [8,9]. But rapid urbanization and industrialization resulted in declining the area suitable for grain production that consequently developed a big challenge to assure food security, particularly in developing countries [10].

Factors Affecting Wheat Growth

Wheat is a member of the family Poaceae, tribe Triticeae and placed in the genus Triticum. It is an annual, long day and self pollinated plant. Wheat is the world most important food crop and covers more cultivated land at the global level than any other crop [11]. Quality characteristics which are important for the utilization of wheat are particularly flour protein concentration, milling yield, rheological properties and bread-making properties. These characteristics usually are influenced by genotype and genotype × environment interactions [12]. Genotype × environment interactions often result into scale or rank shift of genotype overall performance [13,14]. Understanding impenetrable interactions among genotype (crop bio-system) system with the soil, the atmosphere and the environment that plants live in it is important in planning key frame decisions including cultivar selection, sustainable farm management, and economic planning [15,16].

Climate is the major uncontrollable factor that influences crop yield [17]. There are five climatic variables available which include cloud cover, diurnal temperature range, precipitation, temperature and vapours pressure [18]. Since wheat is not grown all year round in every land within Pakistan, we need to account for the seasonal and spatial variation of climate parameters. Janjua et al. [19] analyzed the impact of climate change on wheat production and concluded that higher temperature negatively affected the growth process of wheat thus resulting in severely hampered productivity. A considerable decrease in the number of grains was observed on exposure of floral initiation stage and spikelet development to high temperature conditions thus adversely impacting the maximum yield potential. Sink strength and source capacity are considered two vital factors in modifying the grain yield and quality of wheat genotypes exposed to chronic heat as well as a heat shock [20].

Causes of Climatic Variations

Climate change refers to "change in climate due to natural or anthropogenic activities and this change remain for a long period of time" [21]. The gases responsible for the global warming are known as Green House Gases (GHGs), which are comprised of Carbon Dioxide (CO_2), Methane (CH_4), Nitrous Oxide (N_2O) and water vapors. These gases are produced by a number of anthropogenic activities. Various activities such as deforestation, use of fossil fuels and expanded industrialization etc has increased CO_2 concentration from 280 ppm to 380 ppm [22]. It has been suggested that fluctuations in temperature extremes and water deficit issue will be the key determinants of future climatic conditions. This fact has already been proved in the form of 2003 summer heat wave in Europe where an increase of 5°C above normal temperature was sustained throughout the summer period [23]. As compared to the other living organism plants being motionless have less chance to escape the stress conditions [24].

Heat Stress/ Elevated Temperature

The rise in temperature beyond a certain threshold level for a period sufficient to induce irreversible damage to plant growth and development is referred to as heat stress, where as heat tolerance is the ability of the plants to grow and produce economic yield under high temperatures [25]. Effects of heat (high temperature) stress on different plants were investigated by different scientists such as Lafta et al. [26] on Potato (Solanum tuberosum L.), and Wahid et al. [27] on cereals. Peng et al. [28] reported thatrice yield declined with higher night temperature. Lobell and Asner [29] showed that corn and soybean yield decreased as much as 17% for each degree increase in the growing season temperature.

Effects of Elevated Temperature

Elevated temperature encouraged a theatrical re-setting of physiological and molecular mechanisms in order to help sustained homeostasis and survival [30]. Heat induced oxidative stress is the consequence of production of reactive oxygen species that are formed as a result of damage tomembrane and proteins [31]. Heat can also endorse programmed cell death [32]. Overall these damages may result in reduced photosynthetic rate, impaired translocation of assimilates and reduced carbon gain that ultimately lead to distorted growth and abnormal reproduction [33]. Heat-stress also affects the sensitivity of pigmentation in wheat, maize, and on photosystem II (PS-II) functions in wheat that in turn has lethal impact on seedling growth and leaf development [34-36]. Exposure to higher temperature results in reduced yield and production of inferior quality of cereals [37]. Although all vegetative and reproductive stages are affected by heat stress to some extent yet the stage of plant development also shows varied degree of vulnerability to high temperature [27].

Induction of Heat Shock Proteins (HSPs)

Induction of HSPs seems to be a universal response to temperature stress being observed on all organisms ranging from bacteria to human beings [38]. Higher plants have at least 20 HSPs and same species may have up to 40 different HSPs [39]. The wide diversification and abundance of HSPs in plants reflected the adaptation to temperature stress [40]. HSPs play primary role in thermo-tolerance reactions, prevent denaturation or aggregation of target proteins and facilitate protein refolding [41]. HSPs transcripts were highly up-regulated in response to high temperature in rice [42]. Synthesis of HSPs (100, 78, 70 and 22 kDa) in intact cotton leaves began after 1-h at 41°C [43]. The same authors observed that the HSPs synthesis was more intense under 24-h heat stress. Probably HSPs with a molecular weight of 70 and 78 kDa play a protective role in wheat leaves under heat stress. In wheat, a total of 6560 probe sets displayed a twofold or higher change in expression following a heat treatment of 34°C and/or 40°C. Heat shock proteins in wheat were determined by Xiaozhi et al., Maestri et al., Blumenthat et al., Krishnan et al., Wang et al., Lindquist and Key et al. [44-50].

Combined Effects of Drought and Heat stress

The studies suggested that the combined effects of drought and heat stress had significantly detrimental effects on growth and productivity of crops than separate application of each stress [51]. Moreover, it also alters the physiological processes such as photosynthesis, accumulation of lipids and transcript expression [52,53].

Effect of heat stress on morphology

The manifestation of the adverse effects of drought and heat stress are manifolds including germination, emergence, root, leaf, stem development and growth, tiller, dry matter production, floral initiation, panicle exertion, pollination, fertilization, seed growth, seed yield and seed quality. Like leaf appearance and flowering the rate of germination or seedling emergence can be calculated as the reciprocal of time and has a linear response to temperature [54,55]. Percentage of seed germination under constant soil moisture condition tends to increase with increase in temperature above base temperature (Tb) and reaches its maximum value however it tends to decrease at supra-optimal temperature. Thus the rate and percentage of germination tends to increase as the temperature increases from base to the optimum range and tends to decrease above optimum temperature [56].

Leaf appearance rate is the most affected feature of temperature which commonly implies to the concept of thermal time. Moreover, it is reported that high temperatures are generally involved in regulation of leaf appearance rates and leaf elongation rates along with decreasing leaf-elongation duration [57]. Heat stress also resulted in significant increase in number of leaves, particularly during the arrested reproductive development stage and without any decrease in leaf photosynthetic rate [56]. As compared to other growth processes root growth has a very narrow range of optimum temperature [58]. Decreased number of roots, root length and root diameter are the manifestations of heat stress. Heat stress during reproductive development also retards root growth mainly because of decreased carbon partitioning to the roots [59]. Heat stress also imparts to the decreased seed-filling duration thus resulting in production of smaller seed size [60]. Anthesis stage is considered very crucial with respect to heat stress because the induction of heat stress just before and at this stage showed significant increase in floral abortion and lower number of seeds in peanut, wheat, rice and maize [60-63]. Some legumes such as groundnut, dry bean and cereals showed pollen sterility and loss of seed set when they were exposed to heat stress during flowering stage [64-66]. However, crops such as corn, sorghum, and millet having potential to produce large number of pollen grains and the ability to germinate pollen or grow pollen tube inside the style are more sensitive to environmental stresses. In such species heat and drought stress result in loss of pollen viability which ultimately decrease seed-set if the amount of pollens was limited and/or if anther dehiscence was influenced by stress. Both micro-sporogenesis and mega-sporogenesis are affected under heat stress, resulting in lower seed-set [67]. Studies on maize have suggested that heat stress disrupts cellular and nuclear integrity, particularly in the cells present in the periphery of the endosperm due to mediation of cytokinins [68]. Cytokinins levels which lead to seed abortion cannot be detected in heat stressed plants [69]. Cheikh and Jones [69] reported the presence of relatively stable enzyme cytokinin oxidase whose activity increases under heat stress thus indicating that under stress condition increased stimulation of cytokinin metabolism results in decline in endogenous cytokinin levels. The ability of some crops such as indeterminate soybean, wheat, rice and barley to branch and tiller allows substantial reproductive compensation through seed numbers [70]. However, increased variability in seed size of corn and sunflower is obvious because of selection for one or few inflorescences which may morphologically limit the seed numbers. For instance, in wheat a very strong relation between the vegetative growth and seed numbers is reported, provided that there is no direct influence of drought or heat stress on reproductive process. Likewise, a strong relationship between seed numbers and yield is found when compared with seed-size and yield. Recent review highlights evolutionary tradeoff between seed size and seed number in crops and concludes that seed size is generally more conservative than seed number [70]. Such greater changes and variability in yield components requires greater physiological understanding and analysis of these processes, and even more inquires regarding under stress environments.

Effects of heat stress on plant physiology

Photosynthetic processes depending upon crop species exhibit more tolerance to heat stress with considerable level of stability in the temperature range of 30°C to 35°C, however as the temperature reaches to (>40°C), the process of photosynthesis is affected adversely. Rubisco occupies the central position responding to heat stress due to its temperature sensitive to the two substrates i.e., CO_2 and O_2. High temperature result in the decreased solubility of O_2 and CO_2 however, increased photorespiration and lower photosynthesis is the result of increased level of CO_2 than O_2 [71]. In addition, decreased activity of Rubisco at high temperature is primarily due to inhibition of the enzyme Rubisco activase which becomes unable to overcome the inherently faster rates of Rubisco inactivation [72-74]. Amongst the photosynthetic apparatus photosystem II being more tolerant to drought stress than heat relatively plays a key role in leaf photosynthesis [75]. The sensitivity of photosystem II (PSII) electron transport to heat stress depends on two factors i.e., the increased fluidity of thylakoid at high temperatures leading to dislodging of photosystem II (PSII) light harvesting complexes from thylakoid membrane and the dependence of photosystem II (PSII) integrity on electron dynamics. Hence, in lieu of heat stress metabolic processes either deliver or accept electrons from photosystem II (PSII) that in turn render PSII to be dislodged from thylakoid membrane [75]. A sharp increase in basal level of chlorophyll fluorescence corresponding to photosynthetic inhibition is considered direct indication of inhibition of PSII electron transport under heat stress. Chlorophyll fluorescence measurement tool is of prime importance in quantifying the impact of drought and heat stress on plants [76]. Moreover, mitochondrial respiration is also considered important in determining the growth and survival of plants [77]. One of the most important parameters influencing the mitochondrial respiration is the temperature. The rate of respiration exponentially increases with elevated temperatures from 0 to 35°C or 40°C, reaching plateau at 40°C to 50°C however, at temperatures above 50°C, the rate of respiration decreases as a consequence of destruction of respiratory mechanism. Short term exposure of drought stress can result in decrease in leaf and root respiration [78]. Mitochondria show greater stability to heat stress and their activity increases over most of the temperature range in which plants are grown. However, heat stress is more detrimental to mitochondrial activity than chloroplast activity in some crop species and injured plants because of disrupting growth and maintenance of respiration [79]. Under heat stress conditions the respiratory losses by seeds (grains or kernels) offset the increased influx of assimilates which ultimately account for greater yield losses [80]. Thus, it is crystal clear that increased respiration efficiency and its resistance to heat stress improve growth and yield.

Effect of heat stress on plant biochemistry

Heat stress renders a decrease in total protein content which is due to greater decrease in grain yield rather than protein accumulation [81]. Concentration of protein under heat stress increases during grain filling stage but it significantly decreases the functionality of the protein, which is considered vital for the end-use quality [82]. Heat stress decreases the duration of protein accumulation but did not affect the rate of protein accumulation. Although drought stress during flowering and grain filling often increases protein concentration and viscosity, yet it decreases the flour extraction, flour volume, loaf volume and loaf score during baking [83,84].

Starch granule size, deformed starch granules, and reduced amyloplast numbers are the reported defects of heat stress during post flowering stages [85]. Short-term exposure to heat stress (1 d at 35°C in wheat) results in decreased activity of soluble starch synthase, but further increase in stress duration did not impose any additional impacts [86].

An inverse relationship between grain protein content or product quality traits and grain yield has been recorded [87]. Grain yields are more valuable platforms for the protein and starch yields than the content [88]. Little is known about grain development mechanisms that results in changes in composition and nutritional quality of grains [89]. Daniel and Triboi [90] used a modeling approach to quantify and compare the impact of heat and drought stress on protein aggregation during grain development in wheat in which rate and duration of protein accumulation were calculated as a function of thermal time. Their studies revealed the same effect of temperature and drought on grain weight and on the quality of nitrogen in grains. In comparison to drought stress which decreased the duration both in terms of thermal time and days after anthesis the heat stress decreased the duration of soluble protein accumulation in terms of days after anthesis but not in terms of thermal time. Heat or drought stress did not affect the rate of soluble and insoluble protein accumulation per degree per day that is tantamount to the equations used in a modeling approach. A technique, vegetative index from the spectral reflectance data at the time of anthesis to model grain protein on the basis of remote sensing of leaf nitrogen (N) content using showed strong correlations between the leaf nitrogen (N) content and grain protein content, particularly in wheat [91]. Furthermore, a strong negative relation between the reflectance data and leaf water content was also recorded which proved that grain quality can be estimated on the basis of the reflectance during anthesis stages of wheat particularly under conditions of drought, heat, or N stress. Percentage of shriveled seeds and decreased seed size were also manifestations of heat stress [92]. Seed composition and transcript abundance were also affected by heat stress [93]. Increasing temperatures from optimum 25°C to 28°C, the oil content increased however, above 28°C the oil content declined [94]. In case of soybean seed protein content remained constant at temperatures between 16°C and 25°C but increased at temperatures above 25°C [94,95]. During seed-filling stage the oil and protein concentrations were inversely related in response to heat stress [94]. Pipolo et al. [95] concluded similar quadratic response for oil and protein concentrations of soybean seeds cultured in vitro. A positive correlation was observed between protein and oil concentrations which was a function of rate of dry matter accumulation of soybean seeds. Thus, temperature oriented changes in overall seed-growth rate influences the seed size may, which in turn are likely to be dependent on carbon (C) and N supply to the seeds [95]. Machado and Paulsen [96] studied water relations interactions in response to heat and drought stress and found that water relations adjusted to heat stress when the soil was maintained at field capacity, whereas heat stress interacted strongly with drought and exacerbated its effects when water was withheld. They also highlighted the traits such as enhanced root density and depth, transpiration efficiency, phenology and duration, rapid establishment, early vigor, lower stomatal conductance, slow wilting, leaf angle, leaf reflectance, delayed leaf senescence, accumulation and mobilization of carbohydrates and N to grain, osmotic adjustment, and heat shock proteins and dehydrins important for performance under drought and/or heat stress. Recently, Tewolde et al. [97] while identifying and quantifying the characteristics of wheat cultivars adapted to production systems with risks of heat stress during the post-heading period concluded that early-heading cultivars outperformed later-heading cultivars because the early-heading cultivars had a longer post-heading period and, therefore, a longer grain-filling period than the later-heading cultivars. Additionally, early-heading cultivars would have completed a greater fraction of the grain-filling duration earlier in the season when air temperatures were lower and generally more favorable. The advantage of earlier- heading cultivar was also manifested in the amount of green leaves retained to anthesis. Earlier-heading cultivars produced fewer total leaves per tiller but retained more green leaves and lost fewer leaves to senescence at anthesis than later-heading cultivars. The results suggests that early heading is an important and effective single trait capable of defining wheat cultivars adapted to production systems prone to high temperature stress during post-flowering period. High temperatures during grain filling can significantly alleviate protein concentration while lowering the functionality of protein [82].

Effect of heat stress on wheat

It has been reported that seed germination and seedling emergence in wheat are adversely affected by exposure to heat stress or high temperature [98]. Lower grain weight and altered grain quality are the two reported manifestations of heat stress during the postanthesis grain-filling stage by affecting availability and translocation of photosynthates to the developing kernel, and starch synthesis and deposition within the kernel [99]. Wheat productivity is adversely affected by heat stress in arid, semiarid, tropical and subtropical regions of the world. Effect of heat stress was analyzed by Rahman et al. [100]. Heat stress has negative impact on growth and development of wheat according to various reports [101-103]. Morphological and yield traits were determined by Castro et al., Mohammadi et al., Shah and Paulsen, Viswanathan and Khanna-Chopra, Fokar et al. [104-108]. Heat stress changed the morphology and reduced the grain size, plant height, grain growth duration, kernel number and kernel weight etc.

Effect of heat stress on wheat morphology

The impact of high temperature on characteristics of wheat grains and the protein molecular weight distribution was studied by Castro et al. [104]. High temperatures compact the duration of the grain fill period. Heat stress without taking into account the duration or timing of stress resulted in reduction of thousand kernel weights. Mohammadi et al. [105] reported the effects of post anthesis heat stress on head traits of wheat. Various parameters such as grain filling duration, head weight, kernel number and kernel weight were recorded and compared to the controls. It was observed that heat shock resulted in the reduced grain filling duration, kernel weight and head weight of lines, but the kernel number remained unaffected. Din et al. [109] evaluated the effect of temperature on grain formation and development in ten genotypes of spring wheat. It was observed that as compared to grain yield reduction (53.75%) tillers showed (15.38%) reduction under late planting conditions. Heat stress intensity was high (0.538), which eventually lowered the grain yield under late planting conditions. High heat stress intensity (0.538) was responsible for reduced grain yield under the late planting condition. Viswanathan and Khanna-Chopra [107] reported the reduced grain growth duration and the grain growth rate in wheat varieties experiencing 6-8°C increased temperatures during grain development. The heat tolerance in spring wheat at grain filling stage was checked by Fokar et al. [108]. Considerable variation was seen among cultivars in the reduction in grain weight per ear (RGW), kernel number and single kernel weight under heat stress. High temperature decreased the photosynthetic rate, viable leaf area, shoot and grain mass, kernel weight and sugar content at maturity and reduced water use efficiency as demonstrated by Shah and Paulsen [106].

Effect of heat stress on wheat physiology

Variation in physiological traits for thermo-tolerance in wheat was analyzed by Sing [110]. The ultra structure and biochemical traits of bread and durum wheat grains under heat stress were checked by Dias et al. [111]. Cellular thermo-tolerance is related to yield under heat stress as evaluated according to Blum et al. [112]. Photosynthetic responses of two wheat varieties to high temperature were reported by Efeoglu et al. [113]. Chlorophyll content and stem reserves was done by Mohammadi et al. [114].

Variation in physiological traits for thermo-tolerance in wheat was analyzed by Sing [110]. The wheat cultivars grown under elevated temperature of 35°C showed significant increase in average leaf area (LA), leaf area per shoot, leaf weight ratio (LWR) and leaf length, whereas it reduced the specific leaf weight (SLW), leaf width, plant height, total dry weight and days to flowering and maturity of wheat cultivars. High temperature also increased N content both in leaf and stem at flowering and maturity as well. However, the content of total sugar reduced drastically in shoots both at flowering and maturity stages. The starch content, however, increased markedly in leaf both at flowering and maturity. Wheat cellular thermo-tolerance is related to yield under heat stress as evaluated by Blum et al. [112]. Cellular thermo-tolerance in terms of cellular membrane thermo-stability is often camouflaged as an indication of crop heat tolerance and it is therefore considered as a possible selection criterion for heat tolerance. The ultra-structure and biochemical traits of bread and durum wheat grains under heat stress were checked by Dias et al. [111]. Heat stress, during grain filling, triggered grain shrinkage with a reduced weight and ultra-structural changes in the aleurone layer and in the endosperm cells. It is further recommended that during grain filling, high temperatures might affect gluten strength, diminishing the wheat flour quality. Photosynthetic responses of two wheat varieties to high temperature were reported by Efeoglu et al. [113]. The effects of heat stress at 37°C and 45°C for 8 h on the seedlings of Karacadag and Firat wheat cultivars exhibit that heat stress induced inhibition of chlorophyll accumulation at 45°C for 8 h along with noticeable alterations in the chlorophyll a fluorescence and photosynthesis in the primary leaves of the wheat cultivars at 37°C and 45°C for 8 h. Cultivar Karacadag showed lower reduction in the chlorophyll content and consequently was determined to be a heat tolerant cultivar suitable for cultivation in warmer regions. Selection of bread wheat genotypes tolerant to heat and drought stress based on chlorophyll content and stem reserves was carried out by Mohammadi et al. [114]. Significant correlation was observed between chlorophyll content and grain yield under heat and drought stress that contributed to decrease the drought intensity by reduction of chlorophyll content through light absorption. The heat tolerance in spring wheat and anticipated cellular thermo-tolerance and its heritability was checked by Fokar et al. [108]. Genetic variation in cellular thermo-tolerance among 56 spring wheat cultivars was evaluated at the seedling stage of growth by cell membrane thermo-stability (CMS) and triphenyl tetrazolium chloride (TTC) assays. Results from both assays indicated that average thermo-tolerance tended to decrease from the seedling to the flowering stages.

Effect of heat stress on wheat biochemistry

Stone and Nicolas [81] reported that heat stress increased grain protein percentage despite the fact that protein content per grain was reduced by heat. HSPs in wheat were determined by Xiaozhi et al. [44]. The amount of HSPs induced by a 4 h treatment at 34°C reached the peak. HSPs synthesized at 34°C disappeared after shift of seedlings to 22°C. The synthesis of HSPs was responsible for the acquisition of thermo-tolerance for seedling to survive otherwise lethal temperature.

Expression of gene of HSPs in durum wheat cultivars and acquisition of thermo-tolerance was determined by Rampino et al. [115]. Plants are vulnerable to heat stress and they tend to overcome the vulnerability by modifying their several physiological and biochemical mechanisms. The synthesis of HSPs at the cellular and molecular levels is essential for plants in preventing or minimizing the deleterious effects of extreme temperatures. The two genotypes which were compared in their ability to acquire thermo-tolerance after exposure to different stress conditions were also taken into account for analysis of the expression of HSP101C and four small HSP genes. Variations in HSP transcripts accumulation were noted during the acclimation treatments with concrete evidence that induction of HSP gene expression has a role in the acquisition of thermo-tolerance; determination of moleculargenetics of heat tolerance and HSPs in cereals was done by Maestri et al. [45]. Significance of heat stress response and expression of HSPs in thermo-tolerance of cereal yield and quality has been discussed. Wheat high temperature during grain filling activates the heat shock genes causing the mature grains to contain more protein as proposed by Blumenthal et al. [46] and thus to produce weaker dough. According to Blumenthal et al. [116] wheat coleoptiles exposure to transient high temperature stress results in the synthesis of a group of proteins known as the HSPs. The appearance of these proteins is associated with an associated decline in the synthesis of a normal protein which has been correlated with the acquisition of thermo-tolerance. Krishnan et al. [47] proposed the synthesis of HSPs and thermal tolerance in wheat. The results provide a correlation between the synthesis of specific low molecular weight HSPs and the degree of thermo-tolerance expressed following exposure to elevated temperature. Thermal stress on suspension cell culture in winter wheat was evaluated by Wang et al. [48]. The results directed to infer the differential expression of HSPs genes at different durations of temperature stress in wheat suspension cells and between heat tolerant and heat susceptible genotypes. HSPs according to Lindquist [49] are a set of proteins whose synthesis is induced upon heat stress. The function of the HSPs is as yet unknown. However, evidence suggests that these proteins may provide organisms with a mechanism for thermo-tolerance. HSPs of higher plants were investigated by Key et al. [50]. Rapid and dramatic change in pattern of protein synthesis of soybean seedling takes place with an increase of temperature from 28°C (normal) to about 40°C (heat shock). The synthesis of normal proteins is greatly decreased and a new set of proteins, "heat shock proteins," is induced.

Free amino acids in eight Pakistani wheat varieties differ both qualitatively and quantitatively according to Elahi [117]. Glutemic acids, aspartic acids, phenylalanine, cystine tyrosine, and valine are common to all varieties. Nortino variety contains the greatest amount of free amino acids while C-271 and C-273 contains the least. Ekimovskij [118] performed an experiment to evaluate the free amino acids in spring wheat grain and reached the conclusion that proportion of free amino acids such as tyrosine, alanine and especially tryptophan was more than those of aspartic and glutamic acids, threonine, serine, proline and phenylalanine. The free amino acid content after 122 h of germination was respectively 4 ×, 10 × and 7 × that of the sound wheat at '0 h' Glutamine and proline showed the largest increases according to Tkachuk [119].

Proline enhances the stability of protein and membrane under high temperature or moisture stress according to Mumtaz et al. [120] while Heber and Santarius [121] reported that sugar alcohols improved the stability of membranes and protein to high temperature denaturation however Zhu et al. [122] determined that during the grain filling stage, higher accumulation of proline in stressed leaves occurs signifying that under moderate stress the role of proline is related to a protective action.

Labuschagne et al. [123] determined the influence of temperature extremes on quality of starch in bread, biscuit and durum wheat was checked by. Across the two seasons, in bread wheat, both high and low temperatures resulted in the reduction of weight and diameter of the kernels, thus reducing the starch content to significant levels. In the durum wheat, only heat caused a significant reduction in starch content, which is again reflected in the reduction of kernel weight and diameter. According to Viswanathan et al. [124] wheat varieties differing in grain weight stability when exposed to heat stress showed reduced grain growth duration (GGD) and the grain growth rate. Stable grain starch content was observed in Hindi62 whereas in PBW154 starch content was significantly reduced under heat stress. During grain development of wheat heat stress badly affect the starch content of grain which fallout in poor grain quality, grain size and yield as evaluated by Chinnusamy and Khanna-Chopra [125]. The impact of high temperature on starch accumulation in wheat grains according to Ferris et al. [126] is usually attributed to direct affect of stress on the enzymes involved. Sucrose content of the endosperm as proposed by Jenner [127] was either not affected or amplified by increase in temperature. Increasing temperature has differential effect on glucose and fructose content. Fructose content was reduced whereas glucose content was either unaffected or slightly increased. Response of eight cultivars of wheat to elevated temperature treatment during 60 h greening was examined from the analyses of leaf growth, pigmentation, membrane lipid stability, photosynthesis rates and chlorophyll a fluorescence characteristics of primary leaves was done by Dash et al. [128]. A comparative analysis of parameters revealed the potential of chlorophyll a fluorescence-derived PS II and Rfd index as sensor of heat stress; specifically, the sensitivity of the latter index in screening wheat cultivars at an early developmental growth stage for seedling tolerance against heat-stress.

Thermo-tolerance in Wheat

The acquisition of thermo-tolerance and HSPs gene expression in durum wheat (Triticum durum Desf.) cultivars was studied by Rampinoa et al. [115]. At the cellular and molecular levels, the synthesis of HSPs is essential in preventing or minimizing the toxic effect of high temperature. Evaluation of acquired thermo-tolerance in wheat cultivars grown in turkey was done by Yildiz et al. [129]. Genotypic variability in acquired thermo-tolerance among 30 cultivars of bread (Triticum aestivum L.) and durum (Triticum durum Desf.) wheat was evaluated at the seedling stage of growth by 2,3,5-triphenyltetrazolium chloride (TTC) cell viability and chlorophyll (Chl a+b) accumulation assays. High temperature treatments caused generally less injury to chlorophyll pigmentation of bread wheat cultivars compared to durum wheat cultivars. The decrease in chlorophyll/carotenoid ratio of bread wheat cultivars was lower than that of durum wheat cultivars. TTC and chlorophyll accumulation tests were found to be appropriate for monitoring high temperature stress. The high temperature responses of Aegilops biuncialis species and Triticum durum cultivar was evaluated by Terzioglu et al. [130]. Growth experiment and cell viability tests were implied to estimate the thermo-tolerance of the genotypes and it came to light that most of the HSPs synthesized during acclimation treatment disappeared in response to heat stress in Ae. biuncialis. The bread and durum wheat tolerance to heat stress was determined by Dias et al. [131] which confirmed that increased temperatures during grain filling stage interacts at a metabolic level, growth duration and filling rates, as well as with grain maturity and quality. Screening of wheat germplasm for heat tolerance at terminal growth stage was done by Rehman et al. [100]. The effects of heat stress were lesser in shorter period exposure and more drastic in prolonged exposure of the genotypes to heat. Three entries CB-367 (BB#2/ PT// CC/ INIA /3/ ALD'S'), CB-333 (WL 711/3/KAL/BB//ALD 'S') and CB-335 (WL711/ CROW 'S'//ALD#1/CMH 77A. 917/3/HI 666/PVN 'S') showed maximum grain development and survival. (Note: '/' and '//' represent single and double cross, respectively).

Strategies to Improve Thermo-tolerance in Wheat

High temperature is a severe limiting factor for growth of plants and ultimately effect the grain quality and net productivity of wheat crop. Currently various strategies are being applied to increase thermotolerance in wheat plants. Developments of thermo-tolerant varieties of wheat are one of the major step toward yield improvement of wheat. Additionally to this some other researchers reported tissue culture technique as potent way for better propagation of various plants on large scale [132-136]. There are certain growth enhancers are also being applied exogenously for improvement in germination and post germination potential of wheat [137].

Conclusion

High temperatures causing heat stress in wheat are expected to increase in frequency across the globe. Heat stress substantially affects grain setting, duration and rate, and ultimately grain yield. Nonetheless the timing, duration and intensity of heat stress determine its impact on grain yield. The adversities of heat stress can be minimized by developing tolerant genotypes and agronomic strategies. Even though in wheat, mechanisms of heat tolerance on a physiological basis are relatively well-understood, research into assimilate partitioning and phenotypic flexibility are needed in future.

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