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Physiological traits associated with terminal heat stress in wheat: A review update

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Abstract
Second only to rice as the primary crop for human nourishment, wheat is a significant cereal. The main abiotic stresses that cause significant cellular damage in plant species, including crop plants, are heat, drought, cold, and salinity. These together can cause a significant loss in productivity of wheat. As the predicted increase in global temperature is supposed to jeopardize production, wheat improvement towards heat stress-resilience has gained pivotal importance. Heat stress has a severe negative impact on wheat throughout both the vegetative and reproductive stages; the latter is referred to as terminal heat stress. The creation of wheat genotypes with increased heat tolerance through the fusion of various methods requires rapid attention. Screening of existing genotypes and understanding the variability in these genotypes are the initial task for the breeders to develop heat tolerant wheat. The screening process is made more challenging by the quantitative complexity of heat stress tolerance and environment-sensitive morphological features. So, physico-biochemical approach is more reliable to achieve heat tolerance in wheat. To determine how different physiological characteristics affect heat tolerance, such as better photosynthetic rates, staying green, chlorophyll content (Chl), chlorophyll fluorescence (CFL), membrane thermostability, etc., can be researched. The physiological breeding technique tries to combine features related to all yield determinants to have a genetic effect on production that is cumulative. This review goes into great detail about characteristics for which there is plausible evidence of being heat adaptable.

Keywords: Heat stress, chlorophyll content, synthesis of HSP, chlorophyll fluorescence, plant water status, proline content

Introduction

Wheat (*Triticum spp.*), one of the most significant grain crops, contributes to 50% of the global grain industry and about 30% of grain production worldwide (Akter *et al.* 2017) [1]. A staple crop in more than 40 countries worldwide, wheat provides 85% and 82% of the world's population with their daily protein and calories, respectively (Sharma *et al.* 2019; Chaves *et al.* 2013) [4, 5]. Wheat originated in South-Western Asia, but because of its vast adaptability, it may be produced in a variety of agroclimatic zones, including tropical, subtropical, and temperate zones. With a total area under wheat cultivation of close to 31.5 million hectares, India is the second-largest producer of wheat in the world. Periodic heat stress or continuous stress are considered to be a big risk to wheat, especially in subtropical areas, under all the conditions, notably abiotic factors, generating stress and restricting wheat productivity (Reynolds *et al.* 2016) [2]. Drought is another significant abiotic factor that negatively affects wheat synthesis in many parts of the world (Lesk *et al.* 2016; Liu *et al.* 2016) [6, 7]. Due to the high temperatures, heat stress in wheat is becoming more commonplace worldwide. Heat stress has a severe negative impact on wheat throughout both the vegetative and reproductive stages; the latter is referred to as terminal heat stress. Reduced grain yield is the result of the significant impacts of heat stress on grain setting time and rate. However, the influence of heat stress on grain yield depends on when it occurs, how long it lasts, and how intense it is (Pandey *et al.*

2019) [3] The Intergovernmental Panel on Climate Change (IPCC) estimated that by 2025 and 2100, respectively, temperatures will rise by around 0.3 and 1 degrees Celsius. 13.5 million hectares of wheat in India were impacted by heat stress overall (Joshi *et al.* 2007) [8]. High temperatures have an impact on a variety of physiological, biological, and biochemical processes in wheat (Asseng *et al.* 2015) [9]. Poor seed germination, shorter grain filling times, fewer grains, deactivation of the Rubisco enzyme, decreased photosynthetic capacity, slowed assimilate translocation rates, early leaf senescence, decreased chlorophyll content, and ultimately decreased yield are all effects of heat stress (HS) in wheat (Hossain *et al.* 2013; Din *et al.* 2010) [10, 11]. HS also affects the protein and starch content of grains. According to Mishra *et al.* 2011 [12] and Mittler *et al.* 2011 [13], HS cause the emergence of reactive oxygen species (ROS), which impact membrane integrity as well as lipid peroxidation, protein oxidation, and nucleic acid damage. However, in order to prevent the injury and damage caused by HS, wheat has evolved many tolerance mechanisms to ensure its survival and growth. Heat shock proteins (HSPs) maintain proper protein folding, refolding, and synthesis while also degrading protein aggregates (Sharma *et al.* 2019; Hasanuzzaman *et al.* 2013; Tripp *et al.* 2009) [4, 14, 15]. The antioxidative defense system detoxifies accumulated ROS using several enzymatic and non-enzymatic antioxidants (Sharma *et al.* 2012) [113]. Heat tolerance in wheat is connected with characteristics such as stay green (SG), chlorophyll fluorescence, and canopy temperature

(Pandey *et al*. 2019) [3], high membrane thermo stability (Blum 1988) [16]. There is a lot of room for improvement in heat tolerance because many of the qualities that have been linked to it are heritable, additive in nature, and exhibit continuous variation (Tuberosa and Salvi 2006) [17]. Previously discussed physiological features may be incorporated into breeding plans to help with the selection of parents, generational segregation, or advanced lines who can tolerate heat. The development of wheat cultivars resistant to heat stress in general and terminal heat stress in particular requires a methodical approach. To create effective plant varieties for various climatic situations, breeders must first screen the existing gene pool and investigate untapped genetic diversity (Khodadadi *et al*. 2011) [18]. The screening process is more challenging with environment-sensitive morphological features due to the unpredictable nature of heat stress in the field and the complex quantitative nature of heat stress resistance (Hays *et al*. 2007; Yang *et al*. 2002) [19, 20] Therefore, a trustworthy physic biochemical approach may be required for a rigorous assessment to obtain wheat heat tolerance. Here, we will focus mostly on studying the physiological characteristics of wheat at various phases when there is a lack of water and high temperatures, and we'll try to figure out how to best take advantage of this situation to increase plant productivity and yield.

Impact of heat stress on crop plants
Several reports (Hasanuzzaman *et al*. 2013; Chaudhary *et al*. 2020) [14, 111] explain many adverse effects of heat stress on plant development that impact plant phenology, reproduction, physiology, metabolism, and ultimately economic yield (Wahid *et al*. 2007) [22]. In this review we will discuss the effect of terminal heat stress in physiological process of wheat.

Impact on physiological processes
Photosynthesis, respiration and translocation of metabolites within the plants can be severely affected by heat stress in plant. The sensitivity of Photo System II of various crops to high temperature has been reported in several crops. D1 proteins of the electron transport chain is highly sensitive to extreme temperature (Li *et al*. 2020) [23]. High temperature affects both electron transport and CO_2 fixation processes of photosynthesis. High temperatures have been shown to both increase photorespiration and significantly diminish the activity of calvin cycle enzymes including RuBisCo and RuBisCo activase (Hanumantha *et al*. 2016; Bindumadhava *et al*. 2018) [24, 25]. In crop plants, it can hasten leaf senescence (Kim *et al*. 2020) [26]. Leaf senescence is a common result in heat stressed plants due to degradation of chlorophyll. Tissue degenerating elements within plant cell such as reactive oxygen species (ROS) get activated due to high temperatures (Asthir 2015; Hassan *et al*. 2021) [27, 28]. This is one of the reasons for stress-induced senescence of plant parts. Hence, stay green trait has been proposed as selection criteria for many crops (Kamal *et al*. 2019) [29]. High temperatures change the biochemical makeup of growing grains, which can have a negative impact on grain quality (Akter and Rafiqul 2017) [1]. According to reports on high-temperature tolerance in crop plants (Hasanuzzaman *et al*. 2013; Asthir 2015; Hassan *et al*. 2021) [14, 27, 28], changes

in phenology, anatomy, morphology, metabolism, and physiology of plants ,whether inherent or induced, can help plants escape, avoid, or only temporarily tolerate high-temperature stress at the whole-plant level, organ level or at the cellular level. As the main agent of energy loss, transpiration serves as a crucial mechanism for heat avoidance (Seginer 1994) [30]. Generally speaking, when ambient temperatures rise, so does the transpiration rate, which impacts both evaporation and vapour pressure deficit (VPD). As seen in high-temperature resistant wheat cultivars, the ability to maintain high stomatal conductance at extreme temperatures aids in transpirational heat dissipation. The capacity to withstand high temperatures is linked to ROS scavenging mechanisms, increased photosynthetic apparatus tolerance, and the preservation of membrane stability (Hemantaranjan *et al*. 2014; Das and Roychoudhury 2014; Nadeem *et al*. 2018) [31, 32, 33]. Increased production and recycling of antioxidants and heat shock proteins, which can defend cell organelles and important enzymes, have been linked to biochemical changes (Hasanuzzaman *et al*. 2013) [14].

Numerous physiological characteristics related to wheat's ability to withstand heat are listed below:

Stay green
Vacuolar collapse, cellular homeostasis, and loss of plasma membrane integrity are some of the structural changes that occur in the chloroplast during leaf senescence (Lim *et al*. 2007; Khanna and Chopra 2012) [34, 35]. Leaf senescence is increased in plants that experience significant heat stress throughout their development (Haque *et al*. 2014) [36]. In order to maintain photosynthesis, stay green genotypes postpone the expression of senescence-related genes (Lim *et al*. 2007) [34]. Stay green has been identified as a key of morpho-physiological feature for heat tolerance in wheat. When an abiotic stress occurs it helps plants in keeping their leaves in an active photosynthetic condition (Rosenow DT 1983) [37]. According to the research conducted by Vijayalakshmi and her team, while maintaining greenness is thought to be a stress response mechanism and chlorosis is a crucial component of planned senescence, there are tradeoffs between photosynthesis retained area and nitrogen remobilization of the developing grain. Stay green and high biomass accumulation together with stem water soluble carbohydrate accumulation are likely to affect final green output. According to Spano *et al*. 2003 [38] the stay green traits enable plants continue photosynthesis for a little while longer and keep leaves green. QTLs for the association between remaining green and yielding have been found in population mapping (Kumar *et al*. 2010; Vijayalakshmi *et al*. 2010) [39, 40]. According to Lim *et al*. 2007, when a leaf ages, the chloroplast initially experiences structural changes, followed by regulated vacuolar collapse, followed by the loss of integrity of the plasma membrane and disruption of cellular homeostasis. The association between stay green qualities and canopy temperature depression (CTD) was studied (Dolferus *et al*. 2011) [41]. They discovered that stay green genotypes had higher CTD (air temperature-canopy temperature) values under the heat stressed condition and therefore concluded that stay green is strongly related to CTD. Because of this, the stay green trait in wheat genotypes can be employed as a selection criterion when

exposed to heat stress (Huang *et al.* 2012) [42]. Stay green is a significant strategy for wheat's tolerance to heat stress since it enhances nitrogen remobilization to the ripening grains and conserves photosynthetic regions.

Chlorophyll fluorescence

In order to clarify many elements of the physiological status of photosynthesis in undamaged leaves of higher plants, chlorophyll fluorescence has proven to be a useful and non-damaging instrument. The significance of chlorophyll fluorescence (CFL) in grain productivity under conditions of water stress has been recommended for selecting the wheat genotypes that are resistant to heat and drought. Considering that CFL is directly related to production genotypes with higher yield would have higher CFL values it is possible to use CFL to identify tolerant genotypes. CFL can indirectly predict photosynthetic efficiency in wheat genotypes. The role of CFL & Chl in relation to grain production under water stress has been suggested (Blum 1988; Blum *et al.* 1989) [16, 44] and (Krause and Weis 1991) [45] for the selection of wheat plants for heat and drought tolerance. Fluorescence, which is mostly produced by PS II reaction centers using leaves with dark-adapted chloroplast, causes the reaction center to lose light energy. All of the electron transport channel's intermediate pools for oxidation or reduction revert to their starting concentrations. After an initial surge in light emission from PS II through fluorescence, which is followed by a series of slow oscillations, dark-adapted leaves emit light when lighted. The "Kauntsky effect" (Kautsky *et al.*1960) [46] refers to this. The ratio of the chlorophyll fluorescence variable yield (Fv/Fm), which evaluates photochemical efficiency and represents the efficiency of the light harvesting and electron transport mechanism within the chloroplast, is a requirement for photosynthesis. This varies in relation to the photochemical output of PS II. A decreased level of Fv/Fm on plants indicates biotic or abiotic stress (Spano 2003) [38]. The most delicate component of the photosynthetic system is regarded to be the PS II. The thylakoid is affected by high temperatures, especially PS II, can be shown by a sharp increase in basal fluorescence (Fo).

This increase in basal fluorescence is attributed by Lootens *et al.* 2004 to a functional separation between the PSII reaction center and the LHCII. According to Hassan *et al.* 2021 [28] heat stress reduced photosynthetic rate and resulted in a 26% fall in grain output. Heat stress significantly reduced the amount of chlorophyll fluorescence in wheat plants raised in controlled growth chambers. High temperatures have a negative effect on the photosynthetic processes. Balla *et al.* 2006 [48] found that following anthesis, the amount of N and chlorophyll in wheat flag leaves reduced, and at 14 days after anthesis, the net photosynthetic rate and excitation capture by open PS II reaction centres (Fv/Fm) started to decline. The effects of heat stress at 37 °C and 45 °C for 8 hours on the seedlings of Karacadag and Firat were examined by Banu *et al.* 2009 [49]. Chlorophyll a fluorescence was used to study different wheat varieties. The maximal chlorophyll fluorescence (Fm) and the quantum efficiency of PSII open centers in a dark-adapted condition (FV/FM) drastically decreased when Firat and Karacadag were heat treated.

Canopy temperature depression (CTD)

Reynolds *et al.* 2001 [50] and Araus *et al.* 2003 [51] used the canopy temperature depression (CTD), which is the difference between the temperature of the canopy (Tc) and the surrounding air (Ta), as a proxy for measuring transpiration and plant water status. Infrared thermometers (IRT) have been widely used to measure canopy temperature (CT) directly between the hours of 13:00 and 14:30 without getting too close to the crop. Numerous physiological factors, including stomatal conductance, transpiration rate, plant water status, water use, leaf area index, and crop production, have been linked to CT, according to studies (Yousfi *et al.* 2019) [52]. The canopy temperature is an integrative aspect that, according to Berger *et al.* 2010 [53], indicates the plant's water status or the equilibrium established between root water uptake and shoot transpiration. Stomatal conductance reduces normal transpiration in conditions of strong solar radiation, dryness, and low soil moisture, which boosts canopy temperature (Rebetzke *et al.* 2013) [54]. Therefore, canopy temperature can be used to evaluate how well plant tolerate heat and drought. While the genetic variation in stomatal conductance under heat is linked to the cooler canopy, canopy temperature selection can help improve heat tolerance (Reynolds *et al.,* 1994; 2007) [55]. According to research by Al-Ghzawi *et al.* 2018 [56], canopy temperature depression has been shown to be a quick and reliable test that may be used to choose wheat that is heat resistant. In a study on barley, Awika *et al.* 2017 [57] hypothesised that wax load affects plant canopy temperature and that there is a significant association between epicuticular leaf wax QTL and canopy temperature depression. Recent research reveals that during times of drought and heat stress, canopy temperature is connected to deeper roots (Lopes and Reynolds 2010) [58].

Chlorophyll content

Chlorophyll is a pigment molecule that is crucial to photosynthesis. Since differing chlorophyll molecules in the light harvesting complex capture sunlight, chlorophyll concentration is a crucial determinant of how well plants respond to heat stress. Chlorophyll content and heat stress are tightly connected, and late-sown crops have much lower chlorophyll contents (Tewari 1990) [59]. Chlorophyll loss and heat-induced thylakoid damage are tightly related in winter wheat. Wheat thylakoids suffer damage from heat stress. Wheat high throughput screening for heat tolerance may benefit from measurements of chlorophyll concentration made with a chlorophyll metre (Ristic *et al.* 2007) [60]. In regulated and heat-stressed plants, protochlorophyllide oxidoreductase (POR) concentration was found to be significantly lowered in response to light, according to Mohanty *et al.* 2006 [61]. Fokar (2006) [62] found a significant positive correlation between the rate of photosynthate stem reserves (PSR) and chlorophyll loss under heat stress across cultivars, suggesting that a high potential capacity for using stem reserves for grain filling may be connected with accelerated leaf senescence. According to Wang *et al.* 2008 [63], drought and ion toxicity can hasten the senescence of flag leaves, which lowers chlorophyll concentration and reduces photosynthetic activity. By boosting chlorophyllase activity and decreasing

the concentrations of photosynthetic pigment, heat stress reduces plant photosynthetic and respiratory activities (Todorov *et al.* 2003; Sharkey and Zhang 2010) [64, 65]. In their 2009 study of the physiological reactions of wheat cultivars to high shoot and root temperatures throughout the early growth stages, Tahir *et al.* 2009 [66] came to the conclusion that in most of the measuring dates, chlorophyll accumulation was greatly lowered by NS/HR but enhanced significantly by HS/HR. Under all temperature conditions, the heat-tolerant cultivar Fang always had the highest levels of chlorophyll, Phi PSII, and Pn (Net photosyntheric rate), whereas the heat-sensitive cultivar Siete Cerros always had the greatest drop in these characteristics.

Photosynthesis and Gaseous exchange
Understanding the function of plant response based on physiology for both that is drought and heat is crucial since photosynthesis is a process that is required for both plant growth and crop output. According to report, the main factors limiting photosynthetic rate are decreased photochemical efficiency of photosystem II, biochemical components related to triose-phosphate formation, reduced activity of the photosynthetic enzyme, and earlier stomata closure caused by drought-induced turgor loss (Pandey V. and Shukla A. 2015) [67]. One of the main effects of heat stress is the loss of photosynthesis brought on by the reduced growth of leaf surface area, impaired photosynthesis machinery, pre-maturity that brings on early leaf senescence, and concurrent drop in wheat production (Ashraf and Harris 2013; Mathur *et al.* 2014) [68, 69]. Because photosystem II is negatively impacted by high ambient temperatures, photosynthesis is susceptible to these conditions. The energy necessary for CO_2 fixation can also be impacted by high temperatures (Dusenge *et al.* 2018). RUBisCo activase breakdown reduces photosynthetic capacity under heat stress (Raines CA 2011) [71]. The light harvesting complex II splits from the photosystem II as a result of HS, which also changes the fluidity of the thylakoid membrane (Iwai M *et al.* 2010) [72]. The plant's growth and development depend on the translocation of the photosynthetic product. The rate of assimilate translocation from source to sink is reduced under high temperature stress due to a loss in membrane integrity (Farooq *et al.* 2011) [73].

Plant water relation
Under changing ambient temperatures, plant water status is the most significant variable (Mazorra *et al.* 2002) [74]. When moisture is abundant, plants often maintain consistent tissue hydration status independent of temperature; but, when water is scarce, high temperatures severely hamper this tendency (Machado and Paulsen 2001) [75]. Under field conditions, water availability is typically correlated with severe temperature stress. Numerous variables, including water content, relative water content, water loss rate, succulence index, excised leaf water retention, and transpiration rate residue, can affect a plant's water relations. The most crucial indicator of dehydration tolerance is relative water content (RWC), which assesses the water status of plants and reflects metabolic activity in tissues. A reduction in RWC has been seen as a response to drought stress in a variety of plants (Allahverdiyev *et al.* 2015) [76]. As a result of increased transpiration and decreased osmotic

potential in stressed leaves, dehydration tolerance is linked to several antioxidants that are activated in response to heat stress (Ahmad *et al.* 2010) [11]. In general, increased transpiration during the daytime causes water deficit in plants, resulting in a drop in water potential and the disruption of numerous physiological processes (Tsukaguchi *et al.* 2003) [78]. Heat stress increases the hydraulic conductivity of cell membranes and plant tissues due to an increase in aquaporin activity, and to a greater extent when the water's viscosity is lower (Martinez *et al.* 2009) [79].

Membrane thermo stability
Despite the fact that resistance to high temperatures needs several complex tolerance and avoidance systems (Blum 1988) [16], and despite the fact that membrane damage can be assessed by computing solute leakage from tissue, membranes are recognized as a key location of the physiological harm induced by heat. Thermostability of membranes has been discovered to be a heritable feature in 1998 (Fokar *et al.* 1998) [80]. Membrane thermo-stability (MTS), which measures electrolyte leakage from leaf tissues following exposure to high temperature, was used to assess heat-induced damage to the plasma membrane. The outflow of electrolytes from damaged leaf tissue into an aqueous media can be used as an easy way to evaluate the amount of cellular membrane damage caused by temperature increase (Wahid *et al.* 2007; Govindaraj *et al.* 2018) [22, 82]. For determining sorghum and maize heat tolerance, C.Y. Sullivan developed this approach in the late 1960s (Govindaraj *et al.* 2018) [82]. In wheat (Bala *et al.* 2017; ElBasyoni *et al.* 2017) [83, 84], soybean (Srinivasan *et al.* 1996) [85], maize (Naveed *et al.* 2016) [86] and chickpea (Kumar *et al.* 2013) [39], it has been regularly used to assess cellular thermo stability for heat. Wheat grain weight and membrane injury were shown to be positively correlated, indicating that membrane thermo-stability is a reliable predictor of HS tolerance (ElBasyoni *et al.* 2017) [84]. Based on the proportion of electrolyte leakage in the flag leaves of five different wheat varieties employed the membrane thermo stability test to identify wheat genotypes that are heat resistant. Eight wheat genotypes with different heat tolerance and sensitivity to high temperature stress were examined by Dhanda and Munjal (2009) [87]. According to the findings, choosing heat-tolerant inbred lines based on membrane thermo stability (MTS) in this material would be more successful. Plant breeders are sometimes unable to afford the time and labour required for massive replicates and measurement, which are necessary for success.

Leaf area index
The ratio of the total upper leaf surface of the vegetation divided by the area of the land on which the vegetation grows is known as the Leaf Area Index (LAI). LAI is a dimensionless number.
In their study of the relationship between leaf area index and the pattern of photosynthetically active radiation interception in the profile of wheat canopies, Chinna and Kier (1997) [88] found that the leaf area index (LAI) value increased with crop age and that the upper half of the canopy captured more light than the lower half. According to Mishra (2002) [89], promptly seeded crops (November 22) showed better leaf area indices at various stages than late

sown crops. The wheat variety PBW 343 in the timely seeded crop and the wheat variety UP 2425 in the late sown crop had the highest leaf area index at anthesis. At both the 60 and 75 day stages of her experiment, Tripathi (2003) [90] found that November 28 seeded crops had greater leaf area indices than December 28 sown crops. Compared to a typical sown crop, a late-sown crop had a larger mean tilt angle and gap fraction. According to Nainwal (2007) [91], the crop harvested on November 28 had a greater leaf area index at 50 and 75 days following sowing than the crop harvested on December 20. However, after 50 and 75 days following planting, the mean tilt angel of the crop sown on December 20 was higher than that of the crop sown on November.

Biochemical changes during heat stress
Accumulation of osmolytes
Numerous osmolytes, including as sugars (Such as mannitol, fructans, sorbitol, and trehalose), sugar alcohols (Such as polyols), polyamines (Such as putrescine), quaternary ammonium compounds (Such as glycine-betaine), and amino acids (Such as proline) aid plants in adapting to osmotic stressor (Gepstein *et al.* 2005) [92]. Osmolyte modification has also been used to grow numerous transgenic plants that can withstand heat stress. It has been proposed that using the BADH gene to alter plants could increase their capacity to produce glycine-betaine, which has been linked to increased plant heat tolerance (Yang *et al.* 2005) [93]. Glycine-betaine overabundance has been demonstrated to increase osmotic adjustment and enhance the antioxidant defense system, which includes antioxidative enzymes and antioxidants, in transgenic wheat line T6, improving heat tolerance (Wang *et al.,* 2010) [94]. In response to a variety of challenges, both biotic and abiotic, such as salt stress, water deficiency stress, and severe temperatures, free proline builds up in diverse plants. Proline's role is still unknown, but it is hypothesised that proline accumulation aids in the regulation of cytosolic osmotic pressure under stress, neutralises hydroxyl free radicals, protects protein structure and enzyme activity, and acts as a stress-related signal (Nanzo *et al.* 1999; Hasegava *et al.* 2000) [95, 96]. The functions of proline in osmotolerance in plants are still debatable despite several research in plants. Higher plants experience proline accumulation, which typically occurs in considerable amounts in response to environmental stress. It has been suggested that proline functions as a compatible solute that modifies cytoplasmic osmotic potential. As a result, proline can serve as a metabolic marker in relation to stress (Hare *et al.* 1999; Porgali and Yurekli 2005; Arshi *et al.* 2005) [97, 98, 99].
In response to salinity, heat and their cross-stresses, Song *et al.* 2005 investigated the germination growth of wheat (*Triticum aestivum* L.) seeds and changes in the levels of proline and protein as well as in the activity of key enzymes involved in proline metabolism. Their findings revealed that proline concentration marginally rose as water potential decreased. Vendruscolo *et al.* 2007 [101] and Patel and Vora (1985) [102] both noted higher proline levels in wheat plants during water stress.
Proline levels increased in a number of stress situations, including salinity (Poustini *et al.* 2007) [103], cold (Charest and Phan 1990) [104], UV and high temperature (Tian and Lei 2007) [105], in wheat.

Investigated the relationship between proline level and heat stress (The function of proline in protecting pollen from heat stress), and came to the conclusion that heat injury during floral development of sensitive genotypes may be caused by a decline in proline concentration during the early floral bud development stage and a reduction in the transportation of proline from anther walls to pollen.

Heat stress verses oxidative stress and antioxidants
One of the mechanisms of stress injury in plants is the generation and reaction of reactive oxygen species (ROS), which is why plants have evolved a variety of detoxification systems that break down the extremely toxic ROS. Plants use antioxidase enzymes like superoxide dismutase, ascorbate, peroxidase, glutathione reductase, and catalase to protect their cells from active oxygen radicals.
The activated oxygen species (AOS) that are produced during high heat stress in plants include singlet oxygen ($1O_2$), superoxide radical (O_2), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH). AOS is responsible for the autocatalytic peroxidation of pigments and lipids in membranes. Due to this, membrane semi-permeability is lost (Xu *et al.* 2006) [106]. In general, superoxide radicals are created in small amounts in microbodies in addition to the chloroplast and mitochondrion. Superoxide dismutase (SOD) scavenges oxygen to form H_2O_2, which is then eliminated by APX or CAT. Combination results in hydroxyl radical (OH-), which is created. O_2 and H_2O_2 are significantly more poisonous than each other when produced by the Haber-Weiss reaction in the presence of trace levels of Fe^{2+} and Fe^{3+}. This can destroy essential macromolecules including DNA, lipids, proteins, and chlorophyll, killing the plant (Sairam and Tyagi 2004) [107]. Plants can combat active oxygen species and shield cells from oxidative harm by creating a variety of enzymatic and non-enzymatic detoxification systems (Sairam and Tyagi 2004) [107]. The elimination of H_2O_2, the oxidation of harmful reductants, and other physiological processes are all impacted by excessive SOD expression in plants.
Free radicals are created by oxidation reactions, which can set off a chain reaction and harm cells. These chain reactions are stopped by antioxidants. They have the power to hinder or stop the oxidation of other molecules. A component of heat stress adaptation is the antioxidant defence mechanism. A group of closely related enzymes knew as super oxide dismutase (SODs) aid in the dissociation of the superoxide anion into oxygen and hydrogen peroxide (Bannister 1987) [108].
The ability to develop thermo tolerance in a group of wheat (*Triticum aestivum*) genotypes was associated with catalase and superoxide dismutase activity, a higher ascorbic acid content, and less oxidative damage (Sairam *et al.* 2000) [109]. According to Almeselmani *et al.* 2009 [81] tolerant cultivars have higher SOD activity levels than susceptible cultivars in terms of antioxidant enzyme activity. The peak SOD activity in the late-sown crop was seen 15 days after anthesis. At the vegetative stage, the lowest activity was seen.

Conclusion
Low heritability and the complex character of the major and

minor QTLs controlling them limit the effectiveness of direct selection for yield increase under stressful conditions (Manavalan *et al.* 2009) [110]. The influence of the environment, the complexity and lack of understanding of the genetic inheritance of high-temperature tolerance, and the scarcity of verified QTLs/cloned gene (s) are all obstacles to breeding for combination high yield and heat tolerance (Chaudhary *et al.* 2020) [21]. An ideal strategy for adding high-temperature tolerance gene(s)/QTLs is trait-based breeding. In crop breeding programes, features such canopy structure, delayed senescence, photosynthetic efficiency, lower transpiration rates, resilience in reproductive traits, and the harvest index are utilized to select heat-tolerant accessions (Chaudhary *et al.* 2020) [21]. Selection for traits indirectly linked to yield, such as those conferring high-temperature adaptability, can also be used, as wheat has shown (Cossani and Reynolds 2012) [112]. In wheat and cotton, respectively, chlorophyll fluorescence and canopy temperature depression (CTD) characteristics influenced the ability to withstand high temperatures positively (Sharma *et al.* 2012) [113]. According to Gautam *et al.* 2015 [114], the cooler canopy temperature (CT) under HS increases wheat output. When wheat was under thermal stress, the CTD, flag leaf stomatal conductance, and photosynthetic rate were all positively correlated with yield (Fischer *et al.* 1998) [115]. When assessing genetic variability in various crops, membrane thermo stability has been proven to be a good feature for determining high-temperature tolerance (Shanahan *et al.* 1990; Srinivasan *et al.* 1996) [116, 85]. Therefore, concentrating on a particular physiological feature while breeding is the best method to create genotypes for heat tolerance without reducing yield. In this review, we listed and examined all the physiological characteristics of wheat and other crops that are connected to heat tolerance and can be applied to the breeding of wheat.

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References
1. Akter N, Islam M. Heat stress effects and management in wheat: A review. Agron Sustain Dev. 2017;37:37.
2. Reynolds MP, Quilligan E, Aggarwal PK, Bansal KC, Cavalieri AJ, Chapman SC, *et al*. An integrated approach to maintaining cereal productivity under climate change. Glob Food Sec. 2016;8:9-18.
3. Pandey GC, Mehta GP, Sharma V. Terminal heat tolerance in wheat. Cereal Res Commun. 2019;11(1):1-16.
4. Sharma D, Singh R, Tiwari R, Kumar R, Gupta V. Wheat Responses and Tolerance to Terminal Heat Stress: A Review. In: Hasanuzzaman M, Nahar K, Hossain MA, editors. Wheat Production in Changing Environments: Responses, Adaptation and Tolerance. 2019. p. 149-173.
5. Chaves MS, Martinelli JA, Wesp-Guterres C, Graichen FAS, Brammer SP, Scagliusi SM, *et al*. The importance
6. Lesk C, Rowhani P, Ramankutty N. Influence of extreme weather disasters on global crop production. Nature. 2016;529:84-87.
7. Liu B, Asseng S, Müller C, Ewert F, Elliott J, Lobell DB, *et al*. Similar estimates of temperature impacts on global wheat yield by three independent methods. Nat Clim Change. 2016;12:1130-1136.
8. Joshi AK, Mishra B, Chatrath R, Ferrara GO, Singh RP. Wheat improvement in India: Present status, emerging challenges and future prospects. Euphytica. 2007;157:431-446.
9. Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D, *et al*. Rising temperatures reduce global wheat production. Nat Clim Change. 2015;5(2):143-147.
10. Hossain A, Sarker MAZ, Saifuzzaman M, Silva da JAT, Lozovskaya MV, Akhter MM. Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (*Triticum aestivum* L.) genotypes grown under heat stress. Int J Plant Prod. 2013;7(3):615-636.
11. Din R, Subhani GM, Ahmad N, Hussain M, Rehman AU. Effect of ten temperature on development and grain formation in spring wheat. Pak J Bot. 2010;42(2):899-906.
12. Mishra S, Jha AB, Dubey RS. Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings. Protoplasma. 2011;248:565-577.
13. Mittler R, Vanderauwera S, Suzuki N, Miller GAD, Tognetti VB, Vandepoele K, *et al*. ROS signaling: the new wave. Trends Plant Sci. 2011;16(6):300-309.
14. Hasanuzzaman M, Nahar K, Alam M, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci. 2013;14(5):9643-9684.
15. Tripp J, Mishra SK, Scharf K. Functional dissection of the cytosolic chaperone network in tomato mesophyll protoplasts. Plant Cell Environ. 2009;32:123-133.
16. Blum A. Plant Breeding for Stress Environment. CRC Press. Inc., Boca Raton, Florida; c1988. p. 223.
17. Tuberosa R, Salvi S. Genomics-based approaches to improve drought tolerance of crops. Trends Plant Sci. 2006;11(8):405-412.
18. Khodadadi M, Fotokian MH, Miransari M. Genetic diversity of wheat (*Triticum aestivum* L.) genotypes based on cluster and principal component analyses for breeding strategies. Aust J Crop Sci. 2011;5(1):17-24.
19. Hays DB, Mason RE, Do JH. Developments in plant breeding II. In: Buck HT, Nisi JE, Salomon N, editors. Wheat production in stressed environments. Springer, Dordrecht; 2007.
20. Yang J, Sears RG, Gill BS, Paulsen GM. Quantitative and molecular characterization of heat tolerance in hexaploid wheat. Euphytica. 2002;126(2):275-282.
21. Chaudhary S, Devi P, Bhardwaj A, Jha UC, Sharma KD, Prasad PV, *et al*. Identification and characterization of contrasting genotypes/cultivars for developing heat tolerance in agricultural crops: Current status and prospects. Front Plant Sci. 2020;11:587264.

22. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environ Exp Bot. 2007;61:199-223.

23. Li YT, Xu WW, Ren BZ, Zhao B, Zhang J, Liu P, *et al*. High temperature reduces photosynthesis in maize leaves by damaging chloroplast ultrastructure and photosystem II. J Agron Crop Sci. 2020;206(5):548-564.

24. Hanumantha RB, Nair RM, Nayyar H. Salinity and high temperature tolerance in mungbean [*Vigna radiata* (L.) Wilczek] from a physiological perspective. Front Plant Sci. 2016;7:957.

25. Bindumadhava H, Sharma L, Nair RM, Nayyar H, Riley JJ, Easdown W. High temperature-tolerant mungbean (*Vigna radiata* L.) lines produce better yields when exposed to higher CO2 levels. J Crop Improv. 2018;32(3):418-430.

26. Kim C, Kim SJ, Jeong J, Park E, Oh E, Park YI, *et al*. High ambient temperature accelerates leaf senescence via Phytochrome-Interacting Factor 4 and 5 in Arabidopsis. Mol Cells. 2020;43(7):645.

27. Asthir B. Protective mechanisms of heat tolerance in crop plants. J Plant Interact. 2015;10(1):202-210.

28. Hassan MU, Chattha MU, Khan I, *et al*. Heat stress in cultivated plants: Nature, impact, mechanisms, and mitigation strategies. Int J Plant Biol. 2021;155(2):211-234.

29. Kamal NM, Gorafi YSA, Abdelrahman S, *et al*. Stay-green trait: A prospective approach for yield potential, and drought and heat stress adaptation in globally important cereals. Int J Mol Sci. 2019;20(23):5837.

30. Seginer I. Transpirational cooling of a greenhouse crop with partial ground cover. Agric For Meteorol. 1994;71(3-4):265-281.

31. Hemantaranjan A, Bhanu NA, Singh MN, *et al*. Heat stress responses and thermo tolerance. Adv Plants Agric Res. 2014;1(3):00012.

32. Das K, Roychoudhury A. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Front Environ Sci. 2014;2:53.

33. Nadeem M, Li J, Wang M, *et al*. Unraveling field crops sensitivity to heat stress: Mechanisms, approaches, and future prospects. Agronomy. 2018;8(7):128.

34. Lim PO, Kim HJ, Nam HG. Leaf senescence. Annu Rev Plant Biol. 2007;58:115-136.

35. Khanna CR. Leaf senescence and abiotic stresses share reactive oxygen species mediated chloroplast degradation. Protoplasma. 2012;249:469-481.

36. Haque MS, Kjaer KH, Rosenqvist E, *et al*. Heat stress and recovery of photosystem II efficiency in wheat (*Triticum aestivum* L.) cultivars acclimated to different growth temperatures. Environ Exp Bot. 2014;99:1-8.

37. Rosenow DT. Breeding for resistance to root and stalk rots in Texas. Sorghum root and stalk rots, a critical review. ICRISAT, Patancheru. 1983:209-217.

38. Spano G, Fonzo D, Perrotta N, *et al*. Physiological characterization of 'stay green' mutants in durum wheat. J Exp Bot. 2003;54:1415.

39. Kumar U, Joshi AK, Kumari M, *et al*. Identification of QTLs for stay green trait in wheat (*Triticum aestivum* L.) in the 'Chirya 3' x 'Sonalika' population.

40. Vijayalakshmi K, Fritz AK, Paulsen GM, *et al*. Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. Mol Breed. 2010;26(2):163-175.

41. Dolferus R, Ji X, Richards RA. Abiotic stress and control of grain number in cereals. Plant Sci. 2011;181:331-341.

42. Huang B, Rachmilevitch S, Xu J. Root carbon and protein metabolism associated with heat tolerance. J Exp Bot. 2012;63(9):3455-3465.

43. Gonord F, Santini J, Fanciullino AL, *et al*. Metabolism in orange fruits is driven by photooxidative stress in the leaves. Physiol Plant. 2013;149(2):175-187.

44. Blum A, Shpiler L, Golan G, Mayer J. Yield stability and canopy temperature of wheat genotypes under drought stress. Field Crops Res. 1989;22:289-296.

45. Krause GH, Weis E. Chlorophyll fluorescence and photosynthesis: the basics. Annu Rev Plant Physiol Plant Mol Biol. 1991;42:313-349.

46. Kautsky H, Appel W, Amanh H. Chlorophyll fluorescence and carbon assimilation. Part XIII. The fluorescence and the photochemistry of plants. Biochem Z. 1960;332:277-92.

47. Lootens P, Van WJ, Carlier L. Effect of a short photoinhibition stress on photosynthesis, chlorophyll a fluorescence, and pigment contents of different maize cultivars. Can a rapid and objective stress indicator be found? Photosynthetica. 2004;42(2):187-192.

48. Balla K, Bedo Z, Veisz O. Effect of heat and drought stress on the photosynthetic process of wheat. Cereal Res Commun. 2006;34:381-384.

49. Banu E, Serpil T. Photosynthetic responses of two wheat varieties to high temperature. Eur Asian J Biosci. 2009;3:97-106.

50. Reynolds MP, Nagarajan S, Razzaque MA, Ageeb OAAA. Heat tolerance, in Application of Physiology in Wheat Breeding, eds M.P. Reynolds, and A. McNab (Mexico: CIMMYT) 2001:124-135.

51. Araus JL, Bort J, Steduto P, Villegas D, Royo C. Breeding cereals for Mediterranean conditions: Eco-physiological clues for biotechnology application. Ann Appl Biol. 2003;142:129-141.

52. Yousfi S, Gracia-Romero A, Kellas N, Kaddour M, Chadouli A, Karrou M, *et al*. Combined use of low-cost remote sensing techniques and $\delta^{13}C$ to assess bread wheat grain yield under different water and nitrogen conditions. Agronomy. 2019 Jun;9(6):285.

53. Berger B, Parent B, Tester M. High-throughput shoot imaging to study drought responses. J Exp Bot. 2010 Sep 1;61(13):3519-28.

54. Rebetzke GJ, Rattey AR, Farquhar GD, Richards RA, Condon AG. Genomic regions for canopy temperature and their genetic association with stomatal conductance and grain yield in wheat. Funct Plant Biol. 2013 Jan 18;40(1):14-33.

55. Reynolds MP, Balota M, Delgado MIB, Amani J, Fischer RA. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. Aust J Plant Physiol. 1994 Oct 3;21:717-30.

56. Al-Ghzawi A, Khalaf Y, Al-Ajlouni Z, AL-Quraan N, Musallam I, Hani N. The effect of supplemental

Euphytica. 2010;174:437-445.

irrigation on canopy temperature depression, chlorophyll content, and water use efficiency in three wheat (*Triticum aestivum* L. and T. durum Desf.) varieties grown in dry regions of Jordan. Ag. 2018 May;8(5):67.

57. Awika HO, Hays DB, Mullet JE, Rooney WL, Weers BD. QTL mapping and loci dissection for leaf epicuticular wax load and canopy temperature depression and their association with QTL for stay green in Sorghum bicolor under stress. Euphytica. 2017 Dec 1;213:1-22.

58. Lopes MS, Reynolds MP. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. Funct Plant Biol. 2010 Mar;37:147-156.

59. Tewari SK. Evaluation of productivity constraints of wheat (*Triticum aestivum* L.) under late-sown conditions [PhD thesis]. Pantnagar: G.B Pant University of Agriculture and Technology; c1990.

60. Ristic Z, Bukovnik U, Prasad PVV. Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. Crop Sci. 2007 Sep;47:2067-2073.

61. Mohanty N. Photosynthetic characteristics and enzymatic antioxidant capacity of flag leaf and grain yield in two cultivars of *Triticum aestivum* L exposed to warmer growth condition. J Plant Physiol. 2006 Jan 1;160:71-74.

62. Fokar M, Blum A, Henery T, Nguyen T. Heat tolerance in spring wheat II Grain filling. Euphytica. 2006 May 1;103:9-15.

63. Wang FH, Wang GX, Li XY, Huang JL, Zheng JK. Heredity, physiology and mapping of a chlorophyll content gene of rice (Oryza sativa L.). J Plant Physiol. 2008 Mar 1;165:324-330.

64. Todorov D, Karanov E, Smith AR, Hall MA. Chlorophyllase activity and chlorophyll content in wild and mutant plants of Arabidopsis thaliana. Biol Plant. 2003 Mar;46:125-127.

65. Sharkey TD, Zhang R. High temperature effects on electron and proton circuits of photosynthesis. J Integr Plant Biol. 2010 Aug;52:712-722.

66. Tahir ISA, Nakata N, Yamaguchi T, Nakano J, Ali AM. Physiological response of three wheat cultivars to high shoot and root temperatures during early growth stages. Plant Prod Sci. 2009 Dec;12:409-419.

67. Pandey V, Shukla A. Acclimation and Tolerance Strategies of Rice under Drought Stress. Rice Sci. 2015 Jun;22:147-161.

68. Ashraf M, Harris PJC. Photosynthesis under stressful environments an overview. Photosynthetica. 2013 Mar;51:163-190.

69. Mathur S, Agrawal D, Jajoo A. Photosynthesis response to high temperature stress. J Photochem Photobiol B. 2014 Sep 5;137:116-126.

70. Kalaji HM, Rastogi AZ, Ive AK, Brestic M, Daszkowska-Golec A, Sitko K. Prompt chlorophyll fluorescence as a tool for crop phenotyping: An example of barley landraces exposed to various abiotic stress factors. Photosynthetica. 2018 Dec 1;56:953-961.

71. Raines CA. Increasing photosynthetic carbon assimilation in C3 plants to improve crop yield: Current and future strategies. Plant Physiol. 2011 Feb;155:364.

72. Iwai M, Yokono M, Inada N, Minagawa J. Live-cell imaging of photosystem II antenna dissociation during state transitions. Proc Natl AcadSci USA. 2010 Feb 2;107(5):2337-2342.

73. Farooq M, Bramley H, Palta JA, Siddique KHM. Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sc. 2011 Nov 1;30(6):491-507.

74. Mazorra LM, Nunez M, Echerarria E, Coll F, Sanchez-Blanco MJ. Influence of brassinosteroids and antioxidant enzymes activity in tomato under different temperatures. Plant Biol. 2002 Nov;45:593-596.

75. Machado S, Paulsen GM. Combined effects of drought and high temperature on water relations of wheat and sorghum. Plant Soil. 2001 May 1;233:179-187.

76. Allahverdiyev TI. Effect of drought stress on some physiological parameters, yield, yield components of durum (*Triticum durum* Desf.) and bread (*Triticum aestivum* L.) wheat genotypes. Ekin J Crop Breed Genet. 2015 Jan 31;1:50-62.

77. Ahmed B, Iftikhar RH, Khalil MI, Rahman HU. Genotypic and phenotypic correlation among yield components in bread wheat under normal and late plantings. Sarhad J Agric. 2010;26(2):259-265.

78. Tsukaguchi T, Kawamitsu Y, Takeda H, Suzuki K, Egawa Y. Water status of flower buds and leaves as affected by high temperature in heat tolerant and heat-sensitive cultivars of snapbean (*Phaseolus vulgaris* L.). Plant Prod Sci. 2003;6:4-27.

79. Martinez-Ballesta MC, Lopez-Perez L, Muries B, Munoz-Azcarate O, Carvajal M. Climate change and plant water balance: the role of aquaporins - a review. In: Lichtfouse E, ed. Climate Change, Intercropping, Pest Control and Beneficial Microorganisms. Springer Netherlands; c2009. p. 71-89.

80. Fokar M, Nguyen HT, Blum A. Heat tolerance in spring wheat. I. Genetic variability and heritability of cellular thermotolerance. Euphytica. 1998;104:1-8.

81. Almeselmani M, Deshmukh PS, Sairam RK. High temperature stress tolerance in wheat genotypes: Role of antioxidant defence enzymes. Acta Agronomika Hungarika. 2009;57:1-14.

82. Govindaraj M, Pattanashetti SK, Patne N, Kanatti AA. Breeding Cultivars for Heat Stress Tolerance in Staple Food Crops. Next Generation Plant Breeding. 2018:45-74.

83. Bala P, Lalmia H, Sikde S. Evaluation of heat tolerance of wheat genotypes through membrane thermostability test. J Agric Sci. 2017;2:1-6.

84. ElBasyoni I, Saadalla M, Baenziger S, Bockelman H, Morsy S. Cell membrane stability and association mapping for drought and heat tolerance in a worldwide wheat collection. Sustainability. 2017;9(9):1606.

85. Srinivasan A, Takeda H, Senboku T. Heat tolerance in food legumes as evaluated by cell membrane thermo stability and chlorophyll fluorescence techniques. Euphytica. 1996;88:35-45.

86. Naveed M, Ahsan M, Akram HM, Aslam M, Ahmed N. Measurement of cell membrane thermo-stability and leaf temperature for heat tolerance in maize (*Zea mays* L.): Genotypic variability and inheritance pattern. Maydica. 2016;61(2):7.

87. Dhanda SS, Munjal R. Cell membrane stability: combining ability and gene affects under heat stress conditions. Cereal Res Commun. 2009;37:409-417.

88. Chinna GS, Kler DS. Relationship between leaf area index and photosynthetically active radiation interception pattern in the profile of wheat canopies. Environ Ecol. 1997;15:750-752.

89. Mishra VK. Studies on physiology of heat tolerance in different genotypes of wheat [PhD thesis]. G.B. Pant University of Agriculture and Technology; c2002.

90. Tripathi N. Studies on physiological parameters in relation to heat tolerance in eight wheat varieties [MScAg thesis]. G.B. Pant University of Agriculture and Technology; c2003.

91. Nainwal RC. Effect of sowing dates on seed yield and quality of bread wheat varieties [MSc (Agron.) thesis]. G.B. Pant University of Agric. and Tech.; c2007.

92. Gepstein S, Grover A, Blumwald E. Producing biopharmaceuticals in the desert: building an abiotic stress tolerance in plants for salt, heat and drought. In: Knablein J, Muller RH, eds. Modern Biopharmaceuticals. Wiley-VCH Verlag GmbH; c2005. p. 967-994.

93. Yang X, Liang Z, Lu C. Genetic engineering of the biosynthesis of glycinebetaine enhances photosynthesis against high temperature stress in transgenic tobacco plants. Plant Physiol. 2005;138:2299-2309.

94. Wang GP, Hui Z, Li F, Zhao MR, Zhang J, Wang W. Improvement of heat and drought photosynthetic tolerance in wheat by overaccumulation of glycinebetaine. Plant Biotechnol Rep. 2010;4:213-222.

95. Nanzo T, Kobayashi M, Yoshiba Y, Wada K, Tsukaya H, Kakaubari Y, et al. Biological functions of proline in morphogenesis and osmotolerance revealed in antisense transgenic Arabidopsis thaliana. Plant J. 1999;18:185-193.

96. Hasegava PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. Physiol Mol Biol Plants. 2000;51:463-499.

97. Hare PD, Cress WA, Van SJ. Proline synthesis and degradation: A model for elucidating stress related signal transduction. J Exp Bot. 1999;50:413-434.

98. Porgali ZB, Yurekli F. Salt stress induced alteration in proline accumulation, relative water content and super oxide dismutase (SOD) activity in salt sensitive Lycopersicon esculentum and salt tolerant L. pennelli. Acta Bot Hung. 2005;47:173-182.

99. Arshi A, Abdin MZ, Iqbal M. Ameliorative effects of CaCl2 on growth, ionic relations and proline content of senna under salinity stress. J Plant Nutr. 2005;28:101-125.

100. Song SQ, Lei YB, Tian XR. Proline metabolism and cross-tolerance to salinity and heat stress in germinating wheat seeds. Russ J Plant Physiol. 2005;52:793-800.

101. Vendruscolo ACG, Schuster I, Pilegi M, Scapin CA, Molinari HBC, Viera LGC. Stress induced synthesis of proline confers tolerance to water deficit in transgenic wheat. J Plant Physiol. 2007;165:1367-1376.

102. Patel JA, Vora AB. Free proline accumulation in drought stressed plants. Plant Soil. 1985;84(3):427-429.

103. Poustini K, Siosemardeh A, Ranjbar M. Proline accumulation as a response to salt stress in 30 wheat (Triticum aestivum L.) cultivars differing in salt tolerance. Genet Resour Crop Evil. 2007;54(5):925-934.

104. Charest C, Phan CT. Cold acclimation of wheat (Triticum aestivum): Properties of enzymes involved in proline metabolism. Physiol Plant. 1990;80:159-168.

105. Tian XR, Lei YB. Physiological responses of wheat seedlings to drought and UV-B radiation, effect of exogenous sodium nitroprusside application. Russ J Plant Physiol. 2007;54:676-682.

106. Xu S, Li J, Zhang X, Wei H, Cui L. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass. EEB. 2006;56:274-285.

107. Sairam RK, Tyagi A. Physiology and molecular biology of salinity stress tolerance in plants. Current Science. 2004;86:407-421.

108. Bannister J, Bannister W, Rotilio G. Aspects of the structure, function and applications of superoxide dismutase. Cereal Research Commun. 1987;22:111-80.

109. Sairam RK, Srivastava GC, Saxena DC. Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotypes. Biol Plant. 2000;43:245-251.

110. Manavalan LP, Guttikonda SK, Tran LS, Nguyen HT. Physiological and molecular approaches to improve drought resistance in soybean. JCP. 2009;50:1260-1276.

111. Chaudhary S, Devi P, Bhardwaj A, Jha UC, Sharma KD, Prasad PVV, et al. Identification and characterization of contrasting genotypes/cultivars for developing heat tolerance in agricultural crops: Current status and prospects. Front Plant Sci. 2020;11-587264.

112. Cossani CM, Reynolds MP. Physiological traits for improving heat tolerance in wheat. Plant Physiol. 2012;160:1710-1718.

113. Sharma DK, Andersen SB, Ottosen CO, Rosenqvist E. Phenotyping of wheat cultivars for heat tolerance using chlorophyll a fluorescence. Funct Plant Biol. 2012;39:936-947.

114. Gautam A, SaiPrasad SV, Jajoo A, Ambati D. Canopy temperature as a selection parameter for grain yield and its components in durum wheat under terminal heat stress in latesown conditions. Agric Res. 2015;4(3):238-244.

115. Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Larque Saavedra A. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. Crop Sci. 1998;38:1467-1475.

116. Shanahan JF, Edwards IB, Quick JS, Fenwick JR. Membrane thermostability and heat tolerance of spring wheat. Crop Sci. 1990;30:247-251.

117. Srinivasan A, Takeda H, Senboku T. Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. Euphytica. 1996;88:35-45.