



REVIEW

HEAT STRESS IN WHEAT CROP. PHYSIOLOGICAL, BIOCHEMICAL AND AGRONOMIC IMPLICATIONS

Revisión bibliográfica

Estrés térmico en cultivo del trigo. Implicaciones fisiológicas, bioquímicas y agronómicas

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ABSTRACT. Heat stress in plants trigger responses that affect phenology, physiology, metabolism, and in some cases modify genetic expression, causing variations on agronomic and industrial yield in crops such as wheat. Although not all species and varieties show similar responses to heat stress, monitoring the response of the available germplasm through physiological, biochemical and molecular indicators will allow to identify possible progenitors for genetic improvement, and to recommend tolerant genotypes to regionalize varieties. Given the imminence of climate change that includes significant increases of temperature in several regions where wheat is grown, it is necessary to assess its effects. An important step in this direction is to know the actual state of current research related to the heat stress response. In the present article some heat stress effects on wheat are described due to its importance for human and animal food, and its contributions to the international economy.

RESUMEN. El estrés por altas temperaturas en las plantas origina respuestas que afectan su fenología, fisiología, metabolismo y en algunos casos se modifica la expresión génica, ocasiona variaciones en los rendimientos y la calidad de industrialización de cultivos como el trigo (*Triticum aestivum L.* y *T. durum L.*). Aunque no todas las especies y cultivares responden del mismo modo al calor, el monitoreo de la respuesta del germoplasma disponible a través de indicadores fisiológicos, bioquímicos y moleculares permitirá identificar posibles progenitores para la mejora genética, y recomendar genotipos tolerantes. El cambio climático incluye aumentos significativos de la temperatura en regiones donde se cultiva trigo, por lo cual un paso importante es conocer el estado actual de las investigaciones relacionadas con su respuesta al estrés térmico. En el presente artículo se describen algunos de los efectos del estrés por calor en el cultivo del trigo por su importancia para la alimentación humana y animal, además su contribución a la economía internacional.

Key words: heat, climate change, tolerance, *Triticum*

Palabras clave: calor, cambio climático, tolerancia, *Triticum*

INTRODUCTION

Among the adverse conditions faced by agricultural systems worldwide, high temperature stress is one of the abiotic factors with the greatest impact on the productivity of cultivated plants (1). Approximately 59 % of the world's agricultural land is affected by this stressful condition, which, for the most

part, exceeds the tolerance of traditional crop species (2)^A.

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Thermal stress directly affects crop yield, altering its optimal development, modifying water relations, mainly transpiration rate, photosynthesis-respiration balance, water use efficiency (3), protein synthesis, enzymatic activity and consequently lower agricultural and industrial yields (4). It is currently estimated that wheat will be one of the crops most affected by thermal stress in the next ten years, mainly due to the close relation between yield and cold hours needed by the crop (1).

Among food production strategies in the face of climate change (CC), the use of species and cultivars tolerant to thermal stress is considered of paramount importance and has had special attention in the world during the last five years (1, 5). However, the studies of acclimatization and tolerance still do not meet all expectations, so it will be necessary to work on genetic improvement for this character (6). It is also necessary to develop alternatives such as associations between species and microbial consortia that increase heat tolerance (7, 8).

Studies have shown that yields are reduced by more than 5 % when a 3 °C daytime temperature increase occurs during the phenophase of tillering, and it is generally expected that global wheat production could be reduced by 6 % for each degree centigrade of increase in temperature (1). The polygenic nature of tolerance to abiotic stress in general and thermal stress in particular has been the main limitation for genetic improvement in wheat (9, 10). Therefore, it is necessary to monitor the available germplasm and to identify promising morphological,

physiological, biochemical and agronomic characters in cultivars and species in the face of global climate change scenarios that could be used in improvement programs (11, 12). The present review compiles some of the main research carried out in different latitudes on the physiological, biochemical and agronomic implications of thermal stress in wheat cultivation and discusses the mechanisms for its adaptation and production to such a stressful condition.

METHODOLOGY

The search of documents was carried out in the months of October, 2015 to January, 2016, by academic Google. International standards for the review of published scientific articles were used. The bibliographic review was based on scientific articles, books, book chapters, seminar and congress reports, thesis, and works developed by research centers and universities where wheat cultivation is studied. A total of 62 references were reviewed, mostly related to the cultivation of wheat under conditions of abiotic stress, particularly at high temperatures.

DEVELOPMENT

THE TERM THERMAL STRESS

Thermal stress is defined as the increase in temperature above a certain threshold, for a period sufficient to cause irreversible negative effects on the development and yield of crops (4). High temperatures have a complex effect on many plant species and the final influence on yield will depend heavily on the characteristics of such stress (intensity,

duration or combination with other types of stress), crop (phenological stage and species/genotype) and interaction with other environmental factors (1).

The fluctuations of high temperatures occur in most agricultural regions and it is a common and universal stress that sometimes its effect is not quantified (13). However, it has been estimated that the yield reduction in winter cereals is due to high temperatures during the grain filling period, it could be between 10-15 % (14).

Although the impact of thermal stress has not been evaluated in all regions of the world due to the wide spatial variability of temperatures, it is well established that in traditional agricultural areas increases in the occurrence of thermal stress are expected, and it is predicted that both The daytime and nighttime temperatures will increase between 1,8-5,8 °C in the coming years (15, 16). It has recently been studied that in some crops, such as rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* (L.) Moench) and maize (*Zea mays* L.), high temperatures at night are more harmful than diurnal ones (17 -19).

High temperature stress causes considerable changes in plant morphology and cell ultrastructure (20). The most common morphological effect of this stress type is the increase in the rate of development of the crops and consequently, the reduction in the duration of the phenological stages negatively affects the yield (21). High temperatures significantly affect the permeability of cell membranes in roots (2) and, as a consequence, their selectivity is modified, plant sensitivity increases to the physiological drought condition, and ionic toxicity when other types of Stress such as water stress (22) and saline stress (7).

As membrane permeability is an important factor in the activity of the enzymes associated with it, plant cells have developed mechanisms of thermoregulation by changes in this permeability. Several studies reveal the existence of a positive correlation between the increase in plasma membrane saturation and the tolerance to high temperatures (2, 23).

Plant cells exposed to stress by high temperatures lose the ability to maintain concentration gradients across the membranes and occasionally the osmotic adjustment is modified. This situation is due to the active mobilization of cations (20). In wheat, osmotically active ions (mainly K^+) are accumulated under conditions of thermal stress and organic compounds are synthesized to ensure osmoregulation, including: quaternary amines (glycine betaine, β -alanine, betaine and dimethylsulfonium propionate), amino acids (proline) and various types of sugars (sucrose and mannitol) to decrease osmotic and water potentials and maintain water absorption and transpiration (23). This type of stress damages the membranes by the oxidation of polyunsaturated fatty acids. Lipid peroxidation can occur through enzymatic and free radical pathways (17, 24). The thermostability of membranes based on electrolyte maintenance is an efficient indicator of plant tolerance to thermal stress and it is considered to have a high correlation with yield (25); however, the existence of genetic variability for this character has been demonstrated (26).

GENERAL EFFECT OF THERMAL STRESS

ROOT SYSTEM

In plants subjected to thermal stress, greater elongation and root density have been observed in the region of absorbent hairs. At the same time, there is an increase in its hydraulic conductivity and decrease in the selectivity of Caspary band cells, which favors the hydration of the plant with less energy consumption (26). This response is due to the exploration of more capillary water to maintain perspiration and thermoregulation; however, this propitiates susceptibility to other types of stress such as saline and soil pH (27). These processes are usually regulated among other hormones by ABA (Abscisic acid) (2).

LEAF AREA

Among the main foliar structural modifications under conditions of thermal stress are the reduction of the leaf area, the presence of waxes, the lignification of cuticles and the reduction of the stomatal opening, due to the reduction of the stoma size. This situation leads to decreases in perspiration and photosynthetic activity (26).

DURING THE PRODUCTION

Morphologically during the reproductive stage (tasseling, flowering, filling of grains and maturation), the quantity and size of the flowers are reduced (28), mainly the number of viable flowers (29). There has also been a reported shortening of the culture from the tillering season, accelerating spike appearance, senescence and abscission (29, 30), distal spikelet abortion due to the production of sterile pollen,

decrease in quantity and spike size, grain weight and overall yield (26). The greatest adverse effect of thermal stress in this phenomenon is during formation and filling of the spikelets of the main floral axis (31). This response is due to the increase in ABA concentration, although there are contradictory reports to the above, since during the thermal stress the concentration of gibberellic acid (GA) increases in relation to the ABA, which makes it difficult to fill the grains (32).

PHYSIOLOGICAL PROCESSES MOST AFFECTED BY THERMAL STRESS

Although thermal stress generally affects the morphology and physiology of plants, it has been studied that the processes most affected in this stress condition are: transpiration, photosynthesis and cellular respiration^A.

EFFECTS ON TRANSPIRATION

Under thermal stress, transpiration is more intense but less stable over time (23, 29). In wheat, transpiration is accelerated to ensure thermoregulation, although when the temperature exceeds 25 °C for a time greater than 10 minutes a rapid stomatal closure is observed during the tillering period (33). Some researchers argue that partial or total closure of stomata is not a good adaptive response to thermal stress, since stomatal closure, to avoid water loss, increases the temperature both at the apoplastic and simplistic levels, causing cellular damage (32). This process, like others involved in such a response to thermal stress, is also regulated by abscisic acid (34).

It has been demonstrated that an increase in the temperature in mesophilic cells increases ionic enthalpy by reducing the osmotic potential and consequently the water potential of the cells to absorb more capillary water, a favorable issue to reduce stress (17). However, it causes an additional energy consumption because the opening and closing of the stomata occur actively, an issue that increases cellular respiration (14).

The osmotic adjustment, developed by the plants under conditions of thermal stress, sometimes allows a well hydrated leaf to perspire several times its own volume of water for one day, to achieve the thermoregulation of the parenchyma tissue (8). The plant uses mechanisms to enable homeostasis to open the stoma and, consequently, perspiration and photosynthesis (35).

PHOTOSYNTHESIS

When stomatal closure occurs to reduce the loss of water during transpiration under conditions of thermal stress, it also reduces CO₂ entry which directly affects the photosynthetic process and, in the medium term, yields (35).

The increase in temperature increases the catalytic efficiency of Ribulose 1,5 carboxylase/oxigenase enzyme (RuBisCO) activase, therefore the carboxylation capacity is higher. However, the negative allosteric modulator of the carbon-binding reaction is CO₂, a concentration that can decrease with the active closure of the stomata and affect the carboxylation process (36).

Photosynthesis is one of the most sensitive metabolic pathways to temperature, especially the route of photosystem II.

High temperatures cause disorganization of the "antenna complex", causing changes in the stacking of the granules, alterations in the size and distribution of the membrane components and increase in the permeability of thylakoids. The ability of synthesis and function of chlorophylls also reduces to temperatures above 25 °C in wheat during the tillering (30).

When the temperature is increased above the optimum for the photosynthetic activity it is possible to reach the compensation point quickly, which would affect the performance. At higher temperatures the plant undergoes a net loss of photoassimilates, mobilizes reserve metabolites and inhibits growth (32, 37).

Among the factors that modulate stomatal opening/closure are the CO₂ content in intercellular spaces, relative water content and photosynthetically active radiation. The light induces the opening; on the contrary, a water deficit as well as very high temperatures induces its closure. An extreme increase in temperature causes a decrease in the relative humidity of the air; as well as an increase in the concentration of saturated water vapor and consequently increases perspiration. The plant, in such an adverse situation, to prevent water losses closes its stomas actively (8).

In wheat cultivation, leaf senescence is significantly accelerated under thermal stress conditions due to a significant decrease in "chlorophyll a" content due to the increase in chlorophyllase activity, accelerating chlorophilic catabolism at temperatures above 30 °C (21) and the percentage of leaf cell damage due to desiccation increases due to the loss of the photosynthetically active area (29).

Under high luminous intensity, combined with an increase in leaf temperature, a lateral migration of the Photosystem II complex (LHCII) has been observed (38). This event prevents overexcitation of PSII. High temperatures reduce the electron transport (proportional to saturation by light intensity). It has been observed that high temperatures cause a decline in the electron transport by the PSII in *Triticum durum* L., when the daytime temperatures during the sweetening were 25 °C, which indicates the superiority of tolerance of this species with respect to *T. aestivum* L. (39). Another study indicates that PSII in flour wheats is also affected when the temperature increases by two degrees from 27 °C which significantly affects the photosynthetic apparatus (40).

In relation to carbon assimilation, one of the most marked effects of thermal stress is the RuBisCO activity, since the carboxylation capacity is the biochemical parameter with the highest correlation with the agricultural yield (29, 41). Day temperatures higher than 35 °C significantly reduce the activity of RuBisCO, and as photosynthesis result (42). In general crops exposed to high temperatures, above 5 °C on the optimum exhibit changes in carbon uptake and metabolism (43). These effects include reduced synthesis of structural proteins and increased synthesis of "heat shock" proteins (HSPs), phytohormones (among others ABA) and antioxidants (44). This response may be due to RuBisCO requiring activation that is sensitive to high temperatures.

Thermal stress induces alterations in the RuBisCO quaternary structure, and genetic variability has been found in the tolerance of this enzyme to heat, while the tertiary structure remains stable up to 46 °C (2).

Some studies demonstrate the variability of the oxygenation/ carboxylation enzymatic activity of RuBisCO, with higher oxygenase activity when the temperature is high for more than 72 hours in durum wheat cultivars (27). The regeneration capacity of the RuBisCO is also reduced to high temperatures, aspects that decrease the photosynthetic efficiency (16, 29). The efficiency of the photosynthetic activity under conditions of thermal stress in the filling stage of the grains can be improved with the use of phytohormones such as the brassinosteroids; which confer tolerance for their action on protein synthesis processes with low water availability and increase the efficiency of nitrogen fertilizer use (26).

YIELD

Although wheat yields are polygenic in nature, they are known to be significantly dependent on the efficiency of water use and the photosynthesis/ respiration balance (45). During the thermal stress the respiratory activity and sometimes the photorespiration are accelerated, therefore the energy losses are high. This process is one of the most affected the yield in summer cultivars. Therefore, the physiological improvement has focused mainly on this type of cultivars given the amount of area established to contribute to the production of wheat in different latitudes, where significant temperature fluctuations are already observed as a result of global climate change (46).

The direct relationship between photosynthesis and agricultural yield in wheat has been a contentious issue. There are two complementary approaches to determining yield: (1) yield components and (11) dry matter accumulation and partitioning (47). Due to its simplicity (both conceptual and application in field studies), the approximation of yield components in wheat has been the most used to evaluate the response to abiotic stress conditions in general (46).

High temperatures influence the activity of various enzymes involved in the starch formation in the endosperm (48). It has been observed that the enzymes starch synthetase and ADP-glucose pyrophosphorylase are thermally sensitive and could be responsible for the starch accumulation reduction in wheat under conditions of high temperatures, and therefore those most related to the variation of yield (44). Such enzymes are those that contribute to a good filling of the grains and to a greater quantity of full grains per spike; they are the variables most correlated with agricultural yield (49).

COLD HOURS AND THEIR RELATION TO AGRICULTURAL YIELD

Many species such as wheat need a number of hours of low temperatures during some phenological stages, for the realization of the physiological, biochemical processes and the preparation of their organs for the reproductive stage (29). In wheat, about 300 cold hours are needed to ensure good planting, this process is directly correlated with yield (46). Cultures that do not reach the amount of cold hours required during this phenomenon are likely to decrease their agricultural yield (21).

In regions where temperatures in the low rainy season do not decrease by 10 °C and the total number of cold hours do not exceed 200 hr yields of 5,8 – 6,5 t ha⁻¹ have been achieved under controlled experimental conditions in open field wheat (7), while others with higher cold hours have expressed yields of less than 10 % (49), this demonstrates the variability of response between species.

The biochemical and molecular basis of the number of cold hours is not yet fully described; however, it is assumed that during this stage an imbalance between the ABA-AG hormone ratios is produced from Isopentenylpyrophosphate, an immediate metabolite between the syntheses of these two phytohormones (50). Perhaps some overexpression of a gene or group of them could better explain the response to the needs of a certain amount of cold hours in wheat (51). However, some of the main studies on the interspecific response of wheat to abiotic stress in general indicate that the AABBDD hexaploid wheats are more tolerant than the tetraploids AABB and the AA diploids, which indicates that the genetic factor that controls the tolerance to a certain Amount of cold hours is located in the DD genome and its integration with gene families (AABB) (52, 53).

Various ecological and geographic conditions have been correlated with wheat yields and the number of cold hours and, taking into account the CC scenarios for these latitudes, yield decreases are predicted to be 15%, where wheat producers prefer to establish other crops, an element that threatens the local, regional and global production of cereal^A.

MAIN VULNERABLE BIOCHEMICAL PROCESSES TO HYDRIC STRESS IN WHEAT

From the biochemical point of view, many species of cold climates such as rye and wheat before thermal stress show a common response to develop protective mechanisms against oxidation and thermal denaturation (54). Such is the case of active oxygen species, species that under normal conditions are generated as a consequence of metabolic processes without significant energy implications (38). Reactive oxygen species and their products can reduce photosynthesis and transpiration, accelerate senescence, increase respiration and cause electrolyte flow and can cause genetic mutations in plants when the stress condition is extreme (55).

Oxidative stress is the biochemical state of the cell and tissue where the generation of oxidizing chemical species exceeds the production capacity or activity of antioxidant species (4). It can occur in short or long term and is induced by most types of abiotic stress, as a result of excessive production of active oxygen species, such as singlet oxygen (1O_2), superoxide (O_2^-) radical, The hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH^\cdot) (4). Despite the instability of free radicals, studies have been developed to directly determine their formation, although the nature of the radicals has not always been identified (40). Active oxygen species are formed in several of the cellular organelles. The generation of H_2O_2 can occur from the enzyme NADPH oxidase that is located in the cytoplasmic membrane and the peroxidases of the cell wall in wheat.

Other sources of active oxygen species are electron transport processes in chloroplasts and photooxidative stress in peroxisomes (13).

In order to minimize the toxic effects of active oxygen species, plants have developed highly regulated mechanisms of enzymatic and non-enzymatic protection that trap and inactivate them efficiently to achieve a balance between production and destruction (50).

The ability of plants to overcome oxidative stress due to temperature depends on their ability to trigger such response mechanisms effectively in different cell organelles. Intracellular antioxidants have been characterized better than those located in apoplast and in most species the capacity of antioxidant systems declines as phenology progresses (44).

ENZYMATIC AND NON-ENZYMATIC ANTIOXIDANTS

Among the major enzymatic antioxidants are enzymes that remove toxic oxidants such as superoxide dismutases, peroxidases, catalases and other enzymes that maintain antioxidant levels in their reduced states such as dehydroascorbate reductase, monodehydroascorbate reductase, and glutathione reductase. All these enzymes are activated under conditions of thermal stress to avoid cell damage (29, 44). Currently, little understood are the specific mechanisms that modulate the expression of antioxidant genes under conditions of thermal stress, especially of the genes coding for several isoenzymes of the same protein (56).

Non-enzymatic antioxidants may be lipophilic metabolites, including tocopherols, carotenoids, polyphenols and alkaloids. They may also be hydrophilic, such as glutathione, ascorbate, proline, polyamines and cysteine, which can either directly sequester active oxygen species or serve as substrates for enzyme protection systems (57). In wheat the cysteine proteinase is about 90 % of the total degradation activity of prolamine, (stored protein most abundant in cereals). B-1,3-glucanases (glucan endo-1,3- β -glucosidases) are highly regulated enzymes and widely distributed in the seeds of many plant species, participate in various physiological and developmental processes when stress situations occur The thermal and the saline (58).

In this sense the most efficient defense mechanism is the non-enzymatic system (ascorbic acid, polyphenols, chalcones, tocopherol, anthocyanins, carotenoids, glutathione, among others), but the enzyme system also acts (catalase, peroxidase, ascorbate peroxidase, glutathione reductase, superoxide dismutase, among others), but with energy consumption (59).

Sugars also perform very complex functions during thermal stress and play a vital role in plants (60); In addition to functioning as osmolytes, as energy reserves and as part of the plant structure, are important in different metabolic processes such as transport and signaling (57). Several biochemical and molecular processes affected by thermal stress in wheat during the anthesis and flowering stages involving the reduction of the sugar content in photosynthesis have been explained and accelerated the hydrolysis and mobilization of starch and lipid metabolism (61).

EXPRESSION OF GENES UNDER CONDITIONS OF THERMAL STRESS

To date, several quantitative locus (QTLs) have been identified that are involved in the protection of the cellular structures of various cereals, including the following: *relative growth rate* (CGR), *senescence rate* 2A (10), 6A 6B *greenery during maximum senescence* 4B 5D 3A, 6B *SPAD chlorophyll content* 7B *Fv/Fm fluorescence* 7A, *canopy temperature* 4A and yield 4A (61). (1B, 2B, 3B, 5A, 6D) (56) and *the number of grains* (1A, 2A, 3B, 4A, 5B). In addition, there are genes associated with phenology such as: 2D, 7D (62) and green: 1A, 3B, 7D (53) days, the latter well studied to differentiate lines in breeding programs (55, 62). Thus, the impact of stress on the temperature increase affects several gene groups depending on the genotype and its phenological state (57).

In this way, plants present different strategies to counteract this type of stress, among which the reprogramming of their gene expression, metabolic, or proteomic profiles (58). Thus, transcription factors for the synthesis of NAC (apical meristem) proteins have an important characteristic, a highly conserved N-terminal region, including NAM (non-apical meristem) that allow them to develop during their stress exposure, for example: ATAF1, ATAF2, And CUC2 in *Arabidopsis*. These proteins are generally related to the expression of the response to abiotic stress, mainly due to drought, salinity and heat (59).

Recently, approximately 68,4 % of genes with tolerance expression to thermal and saline stress types have been found (54, 55), demonstrating the existence of genetic variability and considerable heritability in the study of genotypes (53). We are currently working on the identification of genetic variability in germplasm from more precise techniques of cellular and molecular biology such as microsatellites (SSR) and the study of simple nucleotide polymorphisms (SNPs) to undertake breeding programs (60).

CONCLUSIONS

- ◆ High temperatures cause thermal stress in wheat and it is expected that temperatures will continue to rise in the different producing regions of the world. The main damages to the crop occur during the reproductive stage, decreasing the amount of viable pollen consequently the number and weight of grains.
- ◆ Monitoring the response of available germplasm can be an alternative to implement genetic breeding programs and obtain genotypes tolerant to this type of stress in the face of climate change, a question that will increase the production of this important cereal, increase the coefficient of utilization of soils grown in fragile ecosystems that, because of global climate change, have been abandoned because some species and cultivars do not express their productive genetic potential.

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