

Abiotic stress responses and tolerance in wheat under climate change

Éva Darkó, Magda Pál, Tibor Janda*

Department of Plant Physiology; Agricultural Institute, Centre for Agricultural Research, H-2462 Martonvásár, Brunszvik u. 2. HUNGARY

Corresponding author: T. Janda (janda.tibor@atk.hu)

Abstract

Climate change has exacerbated the frequency and severity of many abiotic stresses, particularly water and/or temperature extremities. However, exposure of plants to a mild, non-lethal water stress may activate tolerance mechanisms which help to survive a subsequent severe stress. In the present chapter we focused on the main abiotic stressors, such as low and high temperature stresses, and the osmotic stresses, including drought and high salinity, with special regards to the sensing processes, the acclimation mechanisms and the interactions with the light-mediated processes mainly in wheat. Recent results show that interactions between the different environmental conditions, such as temperature and light might have much more importance in the stress acclimation processes than it was generally assumed. Better understanding of these processes may help to develop stress tolerant plants or methods to improve plant stress tolerance.

Introduction

Different aspects of climate change, such as increasing temperature and air CO₂ level, or changing precipitation may have different effects on crop production. In combination, these effects can both increase or decrease plant production; and the net effect of climate change on crop yield depends on the interactions between these different factors. In the past years, the number of people who suffer from hunger has slowly increased, and approximately 10.8 percent of the total world population still suffers from undernourishment today (FAO 2019). Wheat is one of the leading sources of vegetable protein in human food, having higher protein content than the other major cereals (Chen et al., 2012). As one of the most important plants, wheat is grown on more land area than any other crop all over the world. Its global production is around 6-700 million tons/year. Wheat yields have increased by about a quarter worldwide in the last 10 years. However, in spite of that this is one of the main crop in the world, this is still not enough to reduce the malnutrition of the human population.

Due to the agronomic importance of abiotic stressors, plant breeders and crop producers have an interest in finding crops capable of tolerating environmental changes with as little damage as possible. In order to develop such crops, knowledge of plant defence mechanisms, regulatory processes and genes responsible for stress tolerance is essential. Therefore, understanding of mechanisms by which plant capable to activate adaptive response to environmental stresses not only is of fundamental importance, but also provide important information for breeders. In the present chapter, we focus on the main abiotic stressors, such as temperature stresses (low and high), and the osmotic stresses, including drought and high salinity, with special regards to the sensing processes, the acclimation mechanisms and the interactions with the light-mediated processes.

Temperature stresses

Freezing tolerance

Global climate change causes warming tendency manifesting in mild autumn and winter periods. However, the temperature extremes may also be more frequent, including the number of the sudden frozen days, especially at continental climate. Under these conditions, plants may be less prepared for the winter period, and, in spite of the global warming, they may suffer more severe freezing injury. Wheat plants, having its spring and winter types, grow under widely different climatic conditions, and may show wide differences in freezing tolerance. However, freezing tolerance cannot be developed without acclimation period (e.g. winter wheat varieties also need a certain period of growth at low, but non-freezing temperatures to survive the winter period).

Although changes in the temperature directly affect all the metabolic pathways, the primary cold sensor in plants has not been identified yet. Changes in temperature modify membrane fluidity and in long-term, cells may respond to this with alteration in membrane composition. Changes in triacylglycerol contents and degree of saturation level of fatty acids are associated with cold tolerance in Arabidopsis plants (Arisz et al., 2018). In wheat, the decrease in the trans- Δ^3 -hexadecenoic acid content correlated with the frost tolerance (Szalai et al., 2001). However, adjustment of membrane fluidity is a response to extreme temperatures, it mediates the acclimation processes, but it is probably not the primary sensing mechanism (Lamers et al., 2020). The downstream signalling processes include various cascades with at least partly defined components. One of the main signalling event is related to the Ca^{2+} -dependent processes. In rice, it has been revealed that the so called Chilling tolerant divergence 1 (COLD1) gene containing single nucleotide polymorphisms (SNPs) is responsible for the better cold tolerance in japonica varieties compared with the generally more cold sensitive indica ones. COLD1 encodes a transmembrane protein that interacts with a G-protein resulting enhanced GTPase activity and faster Ca^{2+} influx into the cell upon exposure to low temperatures. (Ma et al., 2015). However, similar differences between spring and winter wheat varieties, at least to our best knowledge, has not been described. The further downstream processes include abscisic acid (ABA)-dependent and ABA-independent pathways. In addition, C-repeat/DRE-Binding Factor (CBF)-dependent and CBF-independent signalling routes are also described, which have been widely studied and reviewed (Park et al., 2018; Yahia et al., 2018).

Studying the cold tolerance mechanisms, it was revealed that growing at low, hardening temperatures itself is not efficient for developing high frost tolerance. Light is also an essential factor contributing to the cold acclimation processes. It has been known for a long time that hardening in the dark, or under low light conditions is much less effective than at normal or high lights (Gray et al., 1997; Apostol et al., 2006). Light mediates the development of freezing tolerance via several acclimation processes, including photosynthesis-related mechanisms, the expression level of stress-related genes and the synthesis of various protective compounds (Janda et al., 2014). A complex interaction has been proposed between cold and light signalling processes (Legris et al., 2017; Szalai et al., 2018). Recent results also showed that both moderate water deficiency and light may also have an influence on nitrogen metabolism and sucrose degradation during cold hardening, indicating a cross-talk mechanism between the different stress responses (Majláth et al., 2016). Results based on wheat or maize plants suggest that photoinhibition occurring under cold conditions, which leads to the over-excitation of the photosynthetic electron transport chain, can be a “necessary evil” for cold acclimation processes in plants (Szalai et al., 2018). However, not only the light intensity, but also the spectral composition affect cold tolerance of plants, indicating that besides the photosynthetic machinery, other light receptors may also contribute to the light-mediated development of cold tolerance (D’Amico-Damião and Carvalho 2018; Ahres et al., 2020). In barley, for instance,

the reduced R:FR ratio increased the frost tolerance independently of light intensity via the modification of the expression of several CBF genes (Ahres et al., 2020). In Arabidopsis, key regulators of light signalling, such as HY5, COP1, and the Z-box regulatory cis-element, mediated by cryptochromes through various interactions with other photoreceptors and signalling molecules are also involved in cold acclimation mechanisms. These regulatory elements are located in the promoter of cold-responsive genes (Mishra and Khurana, 2017).

Figure 1. represents a few main components playing role in temperature/light regulated processes in plants.

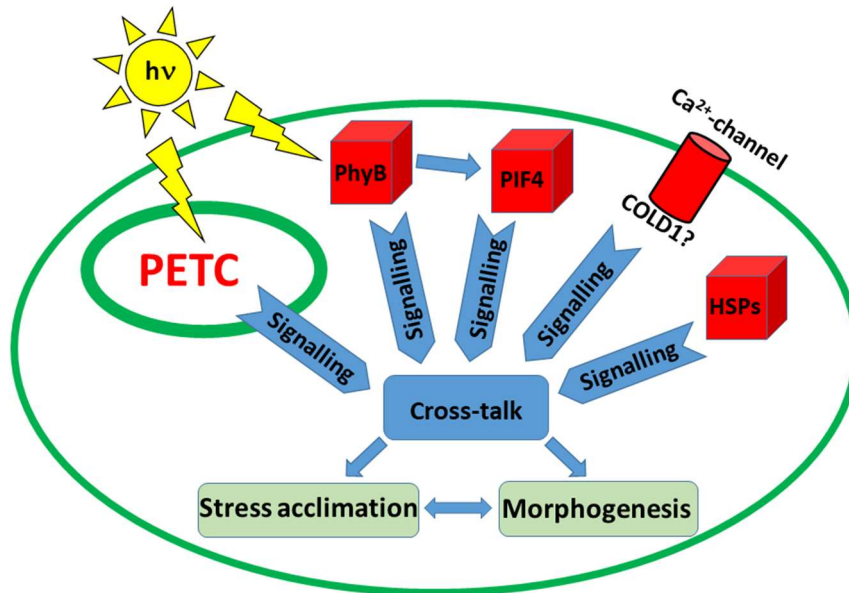


Figure 1. Possible main factors playing key role in light-temperature interactions in plants. PETC: Photosynthetic Electron Transport Chain; PhyB: Phytochrome B. PIF4: Phytochrome Interacting Factor 4.

Elevated temperatures

Climate change, in parallel with global warming (in the last century, the global average surface temperature has increased by more than 0.9 °C), may exacerbate the frequency and severity of a number of other stressors, including extreme high temperature periods, which can significantly reduce the crop productivity. High temperatures affecting various physiological, biochemical, and molecular processes in plants, are one of the most important abiotic stressors that can limit the growth and development of plants in many parts of the world and thus may cause significant economic loss. For example, globally, heat stress can reduce wheat yields by up to 15% (Qin et al., 2008).

Plant cells may sense the elevated temperatures in at least two ways. High temperatures may induce formation of protein aggregates, which can be sensed by Heat Shock Proteins (HSPs). When HSPs bind to aggregated proteins, Heat Shock transcription Factors are released, and they bind to Heat Shock Elements to induce heat-related gene expression. In bread wheat, probably due to its hexaploid genome, the number of HSPs is usually higher than in other grass species (Kumar et al., 2020). However, most of the HSPs are also induced by other stressors, so not all of them may serve as a specific temperature sensor. For instance, light responsive cis-acting regulatory elements was detected in all wheat HSP sub-families which indicates a close relationship between the temperature- and light-regulated processes (Kumar et al., 2020).

Based on results with *Arabidopsis* plants, another sensor can be the red/far-red light receptor Phytochrome B (phyB), which may also sense both light and temperature (Kumar et al., 2012; Legris et al., 2016). High temperatures increase the speed of conversion of activated phyB into the inactive form, resulting in increased stabilization of the transcription factor Phytochrome Interacting Factor4 (PIF4) and hence repression of light-induced gene expression (Lamers et al., 2020). However, these processes are much less known in wheat than in the dicot model plant *Arabidopsis* (Jacott and Boden, 2020). Besides these, it has also been suggested that roots may have an independent thermo-sensing mechanism (Bellstaedt et al., 2019). This is especially important, since as Wang et al (2007) found, wheat roots are more sensitive to heat than shoots.

Under high temperature conditions, the decrease in yield is partly due to limited photosynthetic CO₂ assimilation and increased mitochondrial respiration (Lu et al., 2017). It is known that exposure of plants to moderate elevated temperatures may provide protection against subsequent extreme high temperature stress, thus the so called acquired thermal tolerance is established via heat acclimation or heat priming processes. Several molecular mechanisms are involved in the formation of heat acclimation, including various signalling processes, the synthesis of osmoprotectants and HSPs, and the induction of antioxidant systems (Xu et al., 2006). Pre-anthesis heat priming could also alleviate the photosynthetic injury and oxidative damage caused by post-anthesis heat stress in wheat flag leaves, which was partially attributable to modifications in the expression of the photosynthesis-responsive and antioxidant enzymes-related genes (Wang et al., 2011).

Better understanding of the physiological and molecular mechanisms of heat acclimation is also important from a practical point of view, as these results may also contribute to the production of more heat-tolerant genotypes. In one of our recent works, wheat genotypes of different origins were exposed to heat stress after or without heat priming (Végh et al., 2018). The temperature dependence of certain chlorophyll-*a* fluorescence induction parameters, such as the actual quantum efficiency, the regulated and non-regulated non-photochemical quenching parameters suggested that the temperature-dependent changes in the fluorescence values in acclimated plants starts at higher temperatures than in the non-acclimated ones. These results may indicate the acclimation of the photosynthetic membranes to elevated temperatures. However, fluorescence induction parameters, in contrast to CO₂ assimilation parameters and chlorophyll values, showed less genotype dependence and were more indicative of general acclimatization processes. In contrast, the difference between genotypes in CO₂ assimilation was already evident during acclimatization (Végh et al., 2018). Although slight rise in temperature (acclimatization temperature) does not necessarily induce either stoma closure or photoinhibition, but they may help plants (at least heat tolerant ones) to protect themselves against the negative effects of heat stress with faster stomatal closure at high temperatures. In addition, the activation of several defence processes could be justified; however, not all of them show genotype dependence or direct causal relationship with the stress tolerance of the given plant. Due to the higher transpiration value of the heat-treated plants, significant differences between the control and the heat-treated plants can be shown in water use efficiency. During heat acclimation at 30 °C, wheat plants do not always close their stomata, which would otherwise be the usual response of plants to a number of stressors. This can be important for cooling plants at high temperatures to survive adverse environmental conditions, even if it reduces their water utilization capacity. The more tolerant genotypes, on the other hand, may react more rapidly at extremely high temperatures in regulating gas exchange parameters (Végh et al., 2018). Some previous results indicate that Rubisco activity alone is not particularly sensitive to high temperatures. Other results also show that the sensitivity of Rubisco activity to high temperatures may vary from plant species to plant species. (Law and Crafts-Brandner,

1999), and the primary effect of moderate heat stress on Rubisco activation and photosynthesis may also be primarily due to inhibition of Rubisco activase (Crafts-Brandner and Law, 2000).

Other authors suggested that antioxidant defence mechanisms also play an important role in the adaptation processes of plants to heat stress (Zhao et al., 2014). In addition, in some cases, better heat tolerance was associated with higher antioxidant capacity (Xu et al., 2006, Zhao et al., 2011). Similarly, heat acclimation of winter wheat varieties was associated with an increase in the activity of ascorbate peroxidase and catalase enzymes (Darkó et al., 2019a).

In addition to antioxidant enzymes, polyamines may also play role in adaptation to stress as found in wheat under drought and Cd stress conditions (Pál et al., 2017; Szalai et al., 2017). In case of heat priming the amount of polyamine decreased together with increase of 1,3-diaminopropane, a product of the catabolism of polyamines. These results suggest that the positive effect of heat acclimation cannot be explained by increased polyamine content in wheat. However, the role of signalling processes associated with the polyamine cycle (Pál et al., 2015) cannot be ruled out in the development of heat tolerance (Janda et al., 2019).

Other study also showed that exposure of wheat plants to acclimating high temperatures at pre-anthesis stage improved post-anthesis heat tolerance in the flag leaf via improvement in photosynthesis, enhancement in the activities of antioxidative enzymes and regulation of gene expression at transcription level. The expressions of genes encoding a Rubisco activase or certain superoxide dismutases, and cytosolic glutathione reductase were found to be upregulated in the heat acclimated wheat plants (Wang et al., 2011). In addition, heat acclimation at pre-anthesis stage enhanced the carbohydrate remobilization from stems to grains, improved accumulation of fructans in wheat stem, and maintained grain starch accumulation and starch granule size distribution (Wang et al., 2012). In other studies, the induction of specific biochemical routes, such as synthesis of galactinol contributed the improved heat tolerance in cereals (Janda et al., 2020).

Although the effect of heat stress and the consequences of heat priming is widely investigated many questions remained to be answered in the future: How much time need to develop heat acclimation? The cross-talk of heat priming with other environmental factors (such as light) should also be investigated. This is, for instance, an important question because appropriate balance between the temperature and light intensity is necessary for adequate growth of plants. Furthermore, the adaptation of individual organs and the whole plant may be different, so a detailed study on the role of the root and the crown, for example, is also needed. The stress response also depends on the developmental phase, so further studies are needed to determine whether differences in heat-acclimation processes between genotypes in young plants may also manifest themselves in adult plants with different growth and development stages. Furthermore, vernalisation may also affect the heat acclimation processes, but their relationship is still poorly understood.

Drought and salinity: osmotic stressors

Wheat is cultivated worldwide even in arid and semi-arid regions in spite of the fact most wheat genotype cannot tolerate water shortage. Besides temperature stresses, drought and salinity are also among the most important stressors limiting wheat growth and production in many areas of the world. Worldwide, ca. 60-100 million ha are affected by drought stress, leading to an average grain yield loss of 17–70% (Nouri-Ganbalani et al., 2009), and nearly half of the irrigated land is affected by salinity. The increasing population, shorting of water resources and global warming further increase the problem (Chen et al., 2012).

Both drought and high salinity induce a series of morphological, physiological, biochemical and molecular changes; and among them many are interconnected. The first symptoms of drought and salt stress are related to the reduction of water potential in the cells resulting in loss of turgor, stomatal closure, decrease in the activity of photosynthesis and transpiration. Furthermore, both stressors may cause osmotic and oxidative stresses, which may result in denaturation of functional and structural proteins and membranes leading to the disruption of cellular redox homeostasis. As a consequence, drought and salt stresses often activate similar signal transduction pathways and regulatory genes (encoding transcription factors, protein kinases, protein phosphatases and calmodulin binding proteins, etc.; as summarized in reviews by Wang et al., 2003 and Nezhadahmadi et al., 2013). These stress-induced transcription factors are classified into two groups, ABA dependent and ABA independent ones. The ABA dependent transcription factors include MYC/MYB and ABA responsive element binding/ABA binding factor (AREB/ABF) and the ABA independent transcription factors are dehydration responsive element binding/C-repeat binding factors (DREB/CBF) belonging to the ethylene responsive factor/APETALA2 (ERF/AP2) family (Licausi et al., 2013). As a results of similar cell signalling pathways, the cellular responses, such as the production of stress proteins (e.g. HSPs, LEA, aquaporins), accumulation of osmoprotectants (e.g. prolin, glycine-betaine, sugar polyols) and up-regulation of antioxidants (e.g. ascorbate, glutathione, SOD, etc.) to re-establish cellular homeostasis and maintain the stability of cell are often overlapped (Wang et al., 2003). In spite of the several overlapping mechanisms between drought and salt responses, it must also be mentioned that different osmolytes may also activate different metabolic processes even under iso-osmotic stress conditions and these changes also differed in the leaves and roots (Darkó et al., 2019b). However, either the action or the regulation of these processes have not completely understood yet, even are not integrated with the complexity of whole plant physiology.

Sensing of drought or hyperosmotic conditions is probably related to membrane-bound calcium channels (reviewed by Lamers et al., 2020). Arabidopsis plants contain 15 homologs of reduced hyperosmolality-induced $[Ca^{2+}]_i$ increase 1 (OSCA1) gene encoding calcium channels (Liu et al., 2018), which are responsible for sensing osmotic pressure (Yuan et al., 2014). Besides OSCA genes, several other mechanisms have also suggested as potential sensor for osmotic stress. These may include the Calcium Permeable Stress-Gated Cation Channel1 (AtCSC1A/AtOSCA1.2) as a hyperosmotic stress-induced calcium channel, which may sense for example mannitol, and shows homology with OSCA1 (Hou et al., 2014).

An Arabidopsis mutant called *monocation-induced $[Ca^{2+}]_i$ increases 1 (mocal)* was used to identify MOCA1 as a glucuronosyltransferase for glycosyl inositol phosphorylceramide (GIPC) sphingolipids in the plasma membrane (Jiang et al., 2019). High salinity can be sensed by binding of monovalent cations to the negatively charged glucuronic acid of GIPC. This may lead to opening of an unidentified calcium channel facilitating the calcium influx, which may activate the salt overly sensitive (SOS) systems to exclude excess sodium from the cell.

The restoration of osmotic homeostasis is essential in leaving organisms. In these processes the activation of compatible solutes, including amino acids (e.g. proline), quaternary amines (e.g. glycine betaine, dimethylsulfoniopropanate), sugars (fructose, glucose, sucrose, galactose and trehalose) and sugar alcohols (e.g. mannitol and sorbitol) play important role. However, the synthesis of the compatible solutes differs with respect to cereal species and accessions (Darko et al. 2019a). The primary function of these compatible solutes is to maintain cell turgor and thus the driving gradient for water uptake. However, they can also act as free-radical scavengers or chemical chaperones by directly stabilizing membranes and/or proteins, as well as signalling molecules in stress acclimation processes (Bolouri-Moghaddam et al., 2010). For example, two genes, such as genes of 6-phosphogluconate dehydrogenase and glucose/ribitol dehydrogenase

were identified to be related to osmoregulation under salt stress in barley (Witzel et al., 2010). In wheat, various studies exhibited that wheat genotypes containing higher osmotic regulators have better tolerance to drought (Dhanda et al., 2004) and salt (Zhu 2001).

As secondary effect, both drought and salt induce oxidative stress, against which the plants defend with the increase activity of antioxidant enzymes (such as superoxide dismutase, glutathione reductase, glutathione-S transferase, and ascorbate peroxidase) and with increase of the amount of non-enzymatic compounds (such as ascorbic acid or glutathione). Strong correlation was found in the antioxidant capacity of plants and in their response not only to oxidative stress (Darkó et al., 2009), but also to drought (Darkó et al., 2011) and salt (Sairam et al., 2005). Sucrose metabolism contributes to antioxidant protection as well. It was found that glucose-6-phosphate dehydrogenase may also play a central role in maintaining the reactive oxygen species homeostasis under drought stress through increasing the activities of several antioxidant enzymes, such as glutathione reductase or dehydro-ascorbate reductase as it was demonstrated in soybean plants (Liu et al., 2013).

The role of polyamines in stress responses are also widely investigated. Many reports have indicated that the stress tolerance of plants is correlated with their capacity to enhance the synthesis of polyamines upon exposure to stress. However, the amount of total polyamines and the ratio between individual polyamines vary markedly in dependence of plant species, genotypes and the types of stress (Table 1.).

Table 1. Stress-induced alterations in the major polyamines in various plant species.

Stress	Putrescine	Spermidine	Spermine	Species	References
Cold	Up	Up	Down	rice	Pál et al., 2014
	Up	---	---	maize	Németh et al., 2002
	Up	Up	---	winter wheat	Szalai et al., 2009
	Down	Up	Up	spring wheat	Szalai et al., 2009
	Up	---	Down	Arabidopsis	Cuevas et al., 2008
	Up	Up	Up	chilling tolerant cucumber	Zhang et al., 2009
	Up	Down	---	chilling sensitive cucumber	Zhang et al., 2009
	Up	Up	---	winter barley	Gondor et al., 2016
	Up	Up	---	spring barley	Gondor et al., 2016
	Up	---	Up	spring oat	Gondor et al., 2016
Heat	---	Up	---	tomato	Cheng et al., 2009
	---	---	---	spring barley	Darkó et al., 2019a
	---	---	---	winter barley	Darkó et al., 2019a
	Down	Down	---	spring oat	Darkó et al., 2019a
	Down	Down	---	winter oat	Darkó et al., 2019a
	---	---	Down	heat sensitive wheat	Janda et al., 2019
	---	Down	Down	heat tolerant wheat	Janda et al., 2019
	Up	---	---	white clover	Luo et al., 2020
	Up	Up	Up	tobacco	Todorova et al., 2003

Drought	---	---	Up	rice	Pál et al., 2014
	Up	---	Down	winter wheat	Kovács et al., 2014
	Down	Down	Up	drought tolerant wheat	Doneva et al., 2020
	---	Down	Up	drought sensitive wheat	Doneva et al., 2020
	---	---	---	drought tolerant oat	Canales et al., 2019
	Up	---	Down	drought sensitive oat	Canales et al., 2019
Salt	Down	Down	Down	spinach	Zapata et al., 2004
	Down	Up	Up	lettuce	Zapata et al., 2004
	Down	---	Up	melon	Zapata et al., 2004
	Down	Up	Up	pepper	Zapata et al., 2004
	Down	Up	Up	broccoli	Zapata et al., 2004
	---	Up	---	beetroot	Zapata et al., 2004
	Down	Up	Up	tomato	Zapata et al., 2004
	Down	Down	Up	winter wheat	Darkó et al., 2019b

It is also established that the accumulation of the main polyamines, such as spermine, spermidine and putrescine, and modulation of their biosynthetic pathway also confer tolerance to osmotic stresses induced by drought or high salinity. For example, elevated free spermidine and spermine levels was observed in leaves of drought-tolerant wheat genotypes compared to increased putrescine level in drought sensitive plants in response to PEG-induced osmotic stress (Liu et al., 2007). When the polyamine metabolism was compared under iso-osmotic stress condition induced by PEG or salt treatment in the leaves and roots of a wheat genotype, the total polyamine content increased only in the root under PEG-treatment, but the relative amount of polyamines changed significantly both under PEG-induced drought stress or by salt treatment (Darko et al. 2019b). The amount of putrescine and spermidine decreased, while the amount of spermine increased under salt stress, while PEG-treatment induced the accumulation of putrescine and reduced the amount of spermine and slight changes were found for spermidine. These results suggests that the different polyamine mechanisms operated under salt and PEG treatment even under iso-osmotic stress condition and also differed in the leaves and roots.

The role of polyamines in signalling was also investigated. Recent studies also indicated that polyamines act as cellular signals in intricate cross-talk with hormonal pathways, including ABA regulation in abiotic stress responses (Pál et al., 2015; Pál et al., 2018). Involvement of ABA in the modulation of polyamine biosynthesis has also been demonstrated under water deficit in wheat (Pál et al., 2018). It seems that the ABA is an upstream regulator of polyamine biosynthesis in response to drought. Although recent results indicate that polyamine signalling is involved in direct interactions with other metabolic routes and hormonal cross-talks (Moschou et al., 2008), the precise mechanism by which polyamines control plant responses remained largely unknown. In addition, the hormonal responses, especially the role of ABA in drought and salt stress-induced adaptation process are widely investigated not only in the regulation of stomatal closure, but also in the activation of ABA-dependent signal transduction pathways. Recent results demonstrated that changes in the polyamine pool (Pál et al., 2015) are important for fine tuning of polyamine signalling, which influences the hormonal balance required if putrescine is to exert a protective effect under stress conditions (Szalai et al., 2017).

However, the understanding of the role of hormone metabolism in stress adaptation processes still remained one of the major challenge.

Recent result uncovered many key genes and transcription regulators governing morpho-physiological traits under drought stress conditions. These, among others, include genes controlling root architecture and stomatal development, and therefore can be potential targets of molecular breeding strategies for improving drought tolerance. Although most of the studies were carried out in model plant *Arabidopsis*, for example, WRKY and MYB genes were also identified to be both positive and negative regulators of drought responses in wheat (Kulkarni et al., 2017). Furthermore, several transcription factors were differentially expressed in a drought tolerant wheat genotype compared to sensitive one (Ergen et al., 2009). Similarly to other abiotic stressors, drought and salt tolerances are governed by constitutive and acquired traits. In nature, due to the fluctuating water supply, plants are often exposed to cycles of water stress. Thus, plants after an initial, non-lethal water stress may activate tolerance mechanisms which help to survive a subsequent water stress. However, compared with temperature stresses, the mechanism(s) of acclimation to drought (also called acquired drought tolerance) or high salinity (also called halopriming) is still less studied and less understood.

High level of acquired drought tolerance is especially important for production of crop plant with high water demand under water saving conditions without significant yield loss. A recent comparative phenotyping-based experiment with rice and wheat plants showed that in wheat plants in spite of a decrease in root biomass detected under progressive water stress, a significant increase in root length was observed. Furthermore, wheat plants recovered faster with higher biomass than rice plants, and they were also better able to regulate the amount of reactive oxygen species under drought conditions. It seems that wheat plants may reduce the production of reactive oxygen and carbonyl species through the maintenance of tissue turgor and they are better able to maintain redox homeostasis via increasing scavenging activity to detoxify free radicals than rice plants (Vijayaraghavareddy et al., 2020). A recent study (Amoah et al., 2019) also demonstrated that drought-acclimated plants showed lower level of water loss, hydrogen peroxide and proline accumulations, suffered less membrane damage and decline in photosynthetic pigments. Interestingly, drought acclimation of wheat seedlings resulted in altered metabolic functions at a greater magnitude than the metabolic changes under subsequent severe stress. Substantial induction of the expression of drought responsive genes, namely TaWRKY2, TaNAC1, TaMYB2, TaZIP1, and TaHLLH1 could be detected during the drought acclimation period; however, their induction was already less pronounced during the second phase of stress than in the non-acclimated plants. Results also indicated that the genotypic differences in drought tolerance could be, at least in part, attributed to the ability of plants to acclimate and induce antioxidant defence, enhance growth and water relation, reduced membrane damage, improved photosynthetic activity, and lower gene expression patterns under severe water stress (Amoah et al., 2019).

The contribution of light during drought acclimation or halopriming is less studied than during the cold hardening period. However, adjustment of the physiological processes to fluctuating light intensities under drought conditions is very important for the plants. First, they should avoid the excess photoinhibitory damage of the photosynthetic apparatus, second, they must also optimise the acclimation processes under stress conditions. A recent study using different spring wheat varieties demonstrated the effects of light conditions on structural changes of the photosynthetic machinery during acclimation to water deficit. Novel regulatory mechanisms have also been proposed. One is the acquisition of a drought specific configuration of the photosynthetic machinery, consisting of changes in protein stoichiometry and phosphorylation with the Photosystem 2 or Light Harvesting Complex 2; and the slowdown of decay of non-photochemical quenching upon shift from high to low light (Grieko et al., 2020). Drought-

stressed plants exhibited a reconfiguration of the photosynthetic machinery, they modified the photosynthetic enzymes stoichiometry and the phosphorylation pattern of Photosystem 2. Phosphorylation with the Photosystem 2, including the core and antenna proteins, is an important regulatory mechanism in acclimation to changing light conditions, especially under stress conditions. The level of phosphorylation of the different proteins depends on the level of the stress, and the given plant species. For example, drought stress, induced by PEG increased the phosphorylation of photosystem 2 inner antenna CP29 in barley and maize, but not in spinach (Chen et al., 2009). In drought-stressed wheat plants, CP29 phosphorylation was very low in the phase where there was no photodamage in Photosystem 2. Results also suggested that the modification of Photosystem 2 phosphorylation, accelerating the repair cycle, is a long-term acclimation process for drought conditions (Grieko et al., 2020).

High salinity may induce both osmotic and ionic stresses. Exposure of plant to low salt concentration may provide protection against a subsequent high salinity (salt acclimation or halopriming). Plants can be treated either at seed age by soaking of seeds in salt solution, or young/adult plants can be irrigated with low concentration of salt (Darkó 2020, Janda et al., 2016). Interestingly, halopriming can be induced using both NaCl or other salts. For example, when different salts were compared for priming of wheat seeds, CaSO₄ and CaCl₂ were the most effective in inducing salt tolerance, and NaCl was a less effective priming agent (Afzal et al., 2008). Priming of wheat seeds with calcium salts substantially reduced the sodium accumulation in seedlings, while priming with NaCl enhanced sodium accumulation (Afzal et al., 2008). Interestingly, irrigating of young wheat plants with low concentration of NaCl did not significantly influence the sodium uptake after exposure to high salinity (Janda et al., 2016). Priming with calcium salt increased the levels of total and reducing sugars. However, priming with NaCl had no such an effect (Afzal et al., 2008). It seems that the responses of wheat plants to low concentration, acclimating level of salt and to treatment with high doses of salt may be fundamentally different (Janda et al., 2016). However, the exact mechanisms of halopriming are still poorly understood.

Concluding remarks

In conclusion, acclimation to extreme abiotic stress conditions become more and more an important to survive as the changing environment caused by the global warming for producing enough food for progressively increasing human population. Plants have evolved various mechanisms to sense the changing environment, and to get ready for the further, more extreme conditions. However, the details of the acclimation processes are still poorly understood although the huge amount of data and knowledge about the stress responses of plants increase continuously. These studies demonstrated that storing information about a previous stress event helps plants to response faster and more efficiently in the future then without meeting with a previous stressor. This plant memory is investigated and described at different levels: epigenetic, transcription or metabolic levels. One potential mechanism of memory formation is the sustained alterations in the levels of metabolites, protective compounds, signalling molecules, hormones or transcription factors, which were described in this chapter, such as polyamines, ABA, HSPs, etc. According to these, the recovery period is a critical window, when plant memory can develop. Furthermore, the interactions between the different environmental conditions, such as temperature or light might have much more importance in the stress acclimation processes than it was usually assumed. Better understanding of these processes may help in development of stress tolerant plants or methods using exogenous stress regulators to help plant to be prepared for subsequent stress conditions.

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