sciendo

Agriculture (Poľnohospodárstvo), 67, 2021 (2): 47 – 60

Review

DOI: 10.2478/agri-2021-0005

DROUGHT STRESS IN CEREALS – A REVIEW

MICHAELA HAVRLENTOVÁ[1,2*], JÁN KRAIC[1,2], VERONIKA GREGUSOVÁ[2], BERNADETT KOVÁCSOVÁ[2]

[1]National Agricultural and Food Centre, Lužianky, Slovak Republic
[2]University of Ss. Cyril and Methodius, Trnava, Slovak Republic

Havrlentová, M., Kraic, J., Gregusová, V. and Kovácsová, B. (2021). Drought stress in cereals – A review. *Agriculture (Poľnohospodárstvo), 67*(2), 47 – 60.

Drought is one of the most important factors that influences plant morphology, biochemistry, and physiology, and finally leads to the decline in crops productivity and seed quality. Climate change, severe changes in water availability together with thermal stresses environment coincide with increasing human population, and to reveal sustainable solutions it is necessary to understand: i) how cereals react to drought, ii) how the tolerance mechanisms are exhibited by the genotype, and iii) which approaches enable to increase the tolerance of crop species against limited water availability. Especially in cereals as in high-quality food sources, it is important to reveal the adaptation mechanisms to rainfall dynamics on arable land and to the prolonged period of drought. This review summarizes current knowledge on the impact of drought on cereals, the mechanisms these crops utilize to cope water scarcity and survive, and the most efficient approaches to improve their drought tolerance.

Key words: drought, wheat, dehydrins, abscisic acid, reactive oxygen species, photosynthesis

1. INTRODUCTION

Plants live in a constantly changing environment that often affects their growth and development. They adapt to life under stress conditions by adjusting their physiology, morphology, or metabolism to minimize stress-induced damages. Changes to the plant's biochemical and physiological processes ultimately causing damage to death are considered to plant stress (Atkinson & Urwin 2012). Drought, salinity, and temperature are the major environmental factors, which affect the geographical distribution and productivity of plants (Wang *et al.* 2003; Saradadevi *et al.* 2017; Siddiqui *et al.* 2017; Ghatak *et al.* 2017), quality in agriculture and threaten food (Fedoroff *et al.* 2010; Parkash & Singh 2020).

The impact of abiotic stress continues to have dominant effects on crop production (Lobell *et al.* 2011), whereby only 3.5% of the total land area on Earth is unaffected by environmental factors (FAO 2013). Studies have shown that over the next 30 years, the Earth's average surface temperature will increase by about 0.2°C over a decade. It is estimated that the increase in average global temperature will increase by 2.5 to 4.5°C on average by the end of the 21st century due to increasing concentrations of greenhouse gases (such as CO_2, N_2O, and CH_4) in the atmosphere (Wang *et al.* 2018). The Food and

Michaela Havrlentová (*Corresponding author), Ján Kraic, National Agricultural and Food Centre, Research Institute of Plant Production, Bratislavská cesta 122, 921 68 Piešťany, Slovak Republic. E-mail: michaela.havrlentova@nppc.sk, jan.kraic@nppc.sk
Michaela Havrlentová, Ján Kraic, Veronika Gregusová, Bernadett Kovácsová, University of Ss. Cyril and Methodius, Faculty of Natural Sciences, Department of Biotechnologies, Nám. J. Herdu 2, 917 01 Trnava, Slovak Republic. E-mail: michaela.havrlentova@ucm.sk, bernadett.kovacsova@gmail.com, veronika.gregusova93@gmail.com, jan.kraic@ucm.sk

© 2021 Authors. This is an open access article licensed under the Creative Commons Attribution-NonComercial-NoDerivs License (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Agriculture Organization (FAO) reported in 2018 that 83% of the damage and loss in agriculture as a share of total damage and loss across all sectors in years 2006–2016 was caused by drought (FAO 2018).

Most the plants have very little ability to cope with the environmental conditions in a short term and are extremely vulnerable to acute water shortages.

Wheat (*Triticum aestivum* L.) as the world's most important cereal crop is grown in a large range of latitudes worldwide under both irrigated and rainfed conditions and thus in conditions subjected to drought. Wheat is considered as an excellent system to study drought tolerance in spite of its genetic complexity (Cheng *et al.* 2016).

2. PHYSIOLOGICAL CHANGES IN CEREALS DURING DROUGHT

Water scarcity occurs during drought, where water is simply not present in the soil. Physiological drought is not necessarily caused only by a lack of water in the soil, but it can also occur when there is an excess of water (the soil water potential is lower than in the plant) or high soil salinity (ions also affect the water potential). Thus, physiological drought is a condition where the plant cannot receive water (Lisar *et al.* 2012; Osakabe *et al.* 2014). The responses of plants to water stress are diverse and may involve the contribution of various defence mechanisms or modification of physiology, morphology, anatomy, biochemistry, as well as short and long-term developmental and growth-related adaptation processes (Abobatta 2019).

Physiological responses to drought and heat stresses providing an escape to the water or heat stress comprise morphological and physiological adjustments (Lamaoui *et al.* 2018). Enlarged root system (Gregorová *et al.* 2015; Abobatta 2019), reduced stomatal number and conductance, decreased leaf area, increased leaf thickness, and leaf rolling or folding (Earl & Davis 2003) to lessen evapotranspiration (Anjum *et al.* 2011; Lamaoui *et al.* 2018; Kapoor *et al.* 2020) are strictly associated with an adaptive response. Reduced plant growth and productivity under drought are caused by altered plant water relations, decreased CO_2 assimilation, cellular oxidative stress, membrane damage of affected tissues, and in some cases, inhibition of enzymes activity. Under drought conditions, plants can alter water relations to maintain cellular functions. For example, plants exhibit osmotic adjustment by synthesizing and accumulating compatible solutes such as free amino acids, sugars, and proline (edit some references) (Izanloo *et al.* 2008; Tatar & Gevrek 2008). Osmotic adjustment allows the plant to maintain turgor pressure and cell volume at low water potential which is important for maintaining metabolic functions. In addition, osmotic adjustment facilitates the recovery of metabolic activities after relief from stress (Izanloo *et al.* 2008).

Although investigations have been made to study the recovery of photosynthesis from drought stress (Osakabe *et al.* 2014) in different crop species including wheat, studies addressing membrane stability, oxidative stress, antioxidative process, and osmolyte dynamics during drought recovery are limited. Studies quantifying the impact of plant metabolic changes during drought indicate, that stress conditions during vegetative growth periods can significantly influence grain yield of wheat (Araus *et al.* 2002; Souza *et al.* 2004; Siddiqui *et al.* 2017). After drought stress is removed, the availability of even a small amount of rainfall can have a significant effect on plant physiological functions, ranging from whole-plant physiological and morphological responses to biochemical responses (Abobatta 2019). Therefore, it is of particular importance to investigate the underlying mechanisms contributing to drought tolerance (Izanloo *et al.* 2008).

Water deficit in plants decreases or suppresses the process of photosynthesis (Earl & Davis 2003; Anjum *et al.* 2011; Kapoor *et al.* 2020). The decrease in the photosynthetic process under drought is mainly attributable to the decline in CO_2 conductance via stomata and mesophyll limitations, however, the decrease in photosynthetic activity due to drought may also be due to reduced ability of stomatal movement (Abid *et al.* 2018). The loss of CO_2 uptake affects Rubisco activity and decrease the function of nitrate reductase and sucrose phosphate synthase and the ability for ribulose bisphosphate (RuBP) production (Singh & Thakur 2018).

The chlorophyll content is another photosyn-

thetic attribute strongly influenced by water deficit (Gregorová *et al.* 2015; Alghbari & Iksan 2018). For example, leaf chlorophyll synthesis and chlorophyll *a*/*b* proportion is altered by drought stress. A decline in photosynthetic activity, amount of chlorophylls, loss of photosystem II photochemical efficiency, alteration in stomatal movement, and disturbance in the water status of plants resulted in declined plant productivity. Among others, a major cause for the decline in the amount of chlorophyll due to drought stress is the drought-promoted O^{2-} and H_2O_2 production, which results in lipid peroxidation and significant chlorophyll degradation. Drought stress also causes a reduction in the abundance of several Calvin cycle proteins, including Rubisco (Anjum *et al.* 2011).

In terms of metabolites, a reduced rate of photosynthesis disrupts carbohydrate production, lowers the level of sucrose in leaves, and prevents the transport of sucrose into organs. Ultimately, reproductive development is limited. In addition, drought induces vacuolar inverse of sucrose mediated by hydrolysis and modulation of osmotic potential. Drought inhibits the cell division of the developing embryo/endosperm resulting in the poor intensity of cell division and ultimately leading to germ abortion (Andersen *et al.* 2002).

2.1 Effect of drought on plant growth

Drought stress is well recognized as a limiting factor that alters multiple aspects of plant growth and development (Alghbari & Iksan 2018; Kapoor *et al.* 2020). Germination of seeds, health, coleoptile length, and leaf area are foremost for the plant progression. Seed germination is the primary aspect of growth that is sensitive to drought (Kapoor *et al.* 2020). Visible symptoms of the plant exposed to water scarcity in the initial vegetative stage is besides seed germination reduction also leaf wilting. Plant growth is also in term of reducing shoot length and fresh weight of the hypocotyls negatively affected by lack of water (Abobatta 2019). The interruption in establishment of buds and flowers is also observed due to a lack of nutrients from the dried soil (Abobatta 2019; Kapoor *et al.* 2020). The root system is the main plant organ for adaptation to drought stress conditions. In conditions of water deficit, plants seek to extract water from deeper soil layers by boosting their root architecture (Mitra 2001; Lisar *et al.* 2012; Abobatta 2019). The main basis of variation appears to be constitutive, therefore, a root system architecture that allows reserve of more water quantity is the most important tool for drought tolerance (Abobatta 2019). Moreover, water availability is primarily recognized by roots, which in turn regulates its growth (Kudoyarova *et al.* 2011).

The plant leaf is an important part of the plant because of the process of photosynthesis, which in turn is the main driver of plant growth. Decrease in leaf area is a drought avoidance strategy because declining leaf area results in a decreased water loss by the process of transpiration (Earl & Davis 2003; Anjum *et al.* 2011; Kapoor *et al.* 2020) and this reduction in leaf area is attributable to the inhibition of leaf expansion by the declined rate of cell division, which results in loss of cell turgidity (Xu *et al*. 2010).

Abiotic stress will typically cause upper and lower spikelets and distil florets to either abort or produce small grains (Nuttall *et al.* 2017). A reduction in grain filling occurs due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes (Farooq *et al.* 2009), however, the period and duration of the stress factor is important. Following heading, drought had little effect on the rate of kernel filling in wheat, but its duration (time from fertilisation to maturity) was shortened, and dry weight reduced at maturity (Wardlaw & Willenbrink 2000). In barley, drought stress reduces grain yield by reducing the number of tillers, spikes, grains per plant, and individual grain weight. Post-anthesis drought stress was detrimental to grain yield regardless of the stress severity (Samarah 2005; Alghbari & Iksan 2018). In durum wheat, thousand-grain weight, grain protein yield, and test weight reduced significantly under both salinity and drought stress conditions, whereby salinity stress was greater than drought stress (Houshmand *et al.* 2014).

Soil water deficit condition reduces crop yield by reducing the plant growth according to the following three main mechanisms: i) reduction in canopy absorption of photosynthetically active radiation, ii) decreased radiation use efficiency, and iii) decreased harvest index (Earl & Davis 2003).

2.2 Effect of drought on seed quality

Drought stress leads to the yield losses of major crops worldwide every year (Wang *et al.* 2003; Saradadevi *et al.* 2017; Siddiqui *et al.* 2017). Reducing the availability of water during drought results in a reduction in total nutrient intake and nutrients concentration in plant tissues. A significant impact of the water deficit is manifested in the transport from the perception point, namely from the root system to the above-ground parts (Garg 2003). In general, drought stress induces an increase in nitrogen content (Li *et al.* 2013; Alghabari *et al.* 2018; Magallanes-López *et al.* 2017; Kapoor *et al.* 2020), a definite decrease in phosphorus levels, and does not have significant end effects on potassium content (Garg 2003). During booting and anthesis stages in winter wheat cultivation in a pot experiment under drought stress the concentration of nitrogen and sulphur were observed higher for dwarf cultivars, whereas no significant differences were observed between tall and semi-dwarf wheat cultivars (Alghabari *et al.* 2015).

Starch synthesis is highly sensitive to high temperature and drought stress. Its accumulation in wheat grains can be reduced by over 30% after heat treatment, at temperatures between 30°C and 40°C. Thus, the ability to synthesize, store, and remobilize starch at high temperature is crucial for the determination of grain sink strength (Ni *et al.* 2018). The effects of abiotic stress on the dietary fibre content of wheat and barley grains appear to be variable as one report suggests that β-glucan content of barley decreases under high temperature and drought stress (Savin *et al.* 1997), whereas another reports an increase in β-glucan content under drought stress (Jansen *et al.* 2013).

In durum wheat (*Triticum turgidum* L. var. durum) drought stress affect grain yield, which led to an increase in protein content by linking with better gluten strength and better bread-making quality in the drought environment, although other traits related to gluten quality and content as sodium dodecyl sulfate- (SDS)-sedimentation or mixograph mixing time were somewhat lower in that environment, which indicates probably qualitative changes at the protein level (Li *et al.* 2013; Magallanes-López *et al.* 2017). The analysis of the glutenins composition confirmed different effects of some alleles (Magallanes-López *et al.* 2017). Salt and drought stress in another work with durum wheat grown for two years on the field experiment caused the significant increase in grain protein content, wet and dry gluten contents, and SDS-sedimentation volume, whereby the impact of salinity stress was greater than drought stress (Houshmand *et al.* 2014). Flour protein content and SDS sedimentation volume increased, but not significantly, under drought stress conditions in durum wheat in the work of Li *et al.* (2013). In contrast, the gluten strength-related parameters such as lactic acid retention capacity and mixograph peak time increased significantly under drought. Drought also significantly enhanced flour yellowness (Li *et al.* 2013).

3. MAIN MECHANISMS OF A PLANT TO ADAPT TO DROUGHT CONDITIONS

The common drought-responsive mechanism comprises several characteristics: 1) Drought escape via completing plant life cycle before severe water stress conditions (e.g., early flowering) (Lisar *et al.* 2012; Abobatta 2019). 2) Drought avoidance via enhancing water taking capacity (e.g., developing root systems or conserving water by reducing transpiration such as closure/reduction of stomata and leaf area). 3) Drought tolerance via improving osmotic adjustment and increasing cell wall elasticity to maintain tissue turgidity. 4) Drought resistance via altering metabolic pathways under severe water stress condition. 5) Drought abandonment by reducing/removing a plant part (e.g., shedding mature leaves) (Prasad *et al.* 2017). 6) Drought-prone biochemical-physiological traits for plant evolution under long-term drought condition via genetic mutation and genetic modification (Xu *et al*. 2010). All these mechanisms may be involved consecutively or simultaneously in plant responses to drought stress (Xu *et al*. 2010; Han *et al.* 2015). Generally, C3 plants are better adapt to drought, because the response of C3 species to increased CO_2 is more positive than that of C4 species thanks to increased photosynthetic rate (Araus *et al.* 2002; Hamim 2005). Increased CO_2 increases the water use efficiency of C3 species because it causes a reduction in transpiration rate and an increase in CO_2 assimilation rate

of the plants (Hamim 2005). Studies have also suggested that C3 species may obtain more benefits of CO_2 enrichment under drought stress (Ward *et al.* 1999; Hamim 2005).

One of the most important molecules and best investigated in stress signalling is the plant hormone abscisic acid (ABA) (Davies *et al.* 2005; Daszkowska-Golec & Szarejko 2013; Takahashi *et al.* 2020). Endogenous ABA is rapidly produced in the plant during drought and triggers a cascade of physiological reactions, including stomatal closure (Davies *et al.* 2005) which is regulated by a signal transduction network. Stomatal activity, which is influenced by environmental stress factors, can affect the absorption of CO_2 and thus affect photosynthesis and plant growth (Osakabe *et al.* 2014).

Among proteins, heat-shock proteins (HSPs) (Di Donato & Geisler 2019) and dehydrins (Kosová *et al.* 2013) are involved in plant responses to a drought stress reaction. Chitinases (EC 3.2.1.14) and glucanases (EC 3.2.1.39) are other molecules activated in wheat by drought. Individual isoforms and their activity were rather stimulated under drought, especially in shoots (Gregorová *et al.* 2015).

3.1 Effect of ABA in cereals during drought conditions

Regulation of ABA under drought in plants is well discussed in many studies (Davies *et al.* 2005; Daszkowska-Golec & Szarejko 2013; Ghatak *et al.* 2017; Takahashi *et al.* 2020). However, the detailed molecular mechanisms of stress sensors and the regulators that initiate ABA biosynthesis in response to drought stress conditions are still unclear (Takahashi *et al.* 2020).

Plant roots reflect to the drying soil and produce signals, while ABA on transmission to shoots triggers stomatal closure to regulate crop water use through transpiration. However, transpiration is linked to crop growth and productivity, and limiting transpiration may reduce potential yield. While an early and high degree of stomatal closure affects photosynthesis (Osakabe *et al.* 2014) and hence biomass production, a late and low degree of stomatal closure exhausts available soil water rapidly which results in yield losses through a reduction in post-anthesis water use. Wheat genotypes differ in their ability to produce ABA under drought conditions and also in their stomatal sensitivity to ABA. Root density distribution in the upper drying layers of the soil profile is identified as a candidate trait that can affect ABA accumulation and subsequent stomatal closure (Daszkowska-Golec & Szarejko 2013; Saradadevi *et al.* 2017). A simple collection of leaf samples to quantify ABA compared to extracting xylem tissue will facilitate rapid screening of a large number of germplasm for drought tolerance (Saradadevi *et al.* 2017).

An increased concentration of ABA in leaves associated with reduced stomatal conductance under water deficits has been confirmed in several studies conducted in various species including wheat (Saradadevi *et al.* 2017). A higher concentration of ABA was observed in wheat roots in association with increased root hydraulic conductance following excision of four out of five seminal roots. This increased concentration of ABA in root and subsequent enhancement of root hydraulic conductivity to meet increased transpiration demand is due to the redistribution of ABA from leaf to root (Kudoyarova *et al.* 2011). Thus, leaf ABA is involved in regulating root hydraulic conductivity, in addition to its role in regulating stomata (Saradadevi *et al.* 2017).

ABA has a central role in root-to-shoot drought stress signalling (Davies *et al.* 2005; Takahashi *et al.* 2020) and the regulation of functioning, growth, and development of plants in drying soil (Davies *et al.* 2005). Changes in xylem and apoplastic pH can affect the way in which ABA regulates stomatal behaviour and growth (Davies *et al.* 2005).

The lack of consensus among researchers in relation to a positive, negative, or neutral influence of ABA on grain yield suggests that the timing at which the water stress occurs is important. Pre-anthesis water stress, particularly during spike development and pollen meiosis, reduces grain number while post-anthesis water stress reduces grain size (Dolferus *et al.* 2011). This is because high ABA levels during the early reproductive stage affect grain composition and reduce grain number. On the other hand, during post-anthesis stages, high ABA levels promote grain filling by redistributing reserved carbohydrates to the grain (Liu *et al.* 2005). In one of the recent studies, when the soil water was exhausted rapidly after anthesis, the wheat cultivar Drysdale maintained a higher grain yield with a higher harvest index and

grain weight compared to the advanced drought-tolerant line IGW-3262. This was mainly because the cultivar Drysdale was more efficient at translocation of assimilates to grain (Saradadevi *et al.* 2015). Based on this study it appears that ABA negatively affects grain composition, but has a positive effect on grain filling by facilitating assimilate distribution to grain (Saradadevi *et al.* 2017).

3.2 The importance of HSPs in plant protection during drought

Heat shock proteins (HSPs) are a major component of multiple stress responses in plants (Guo *et al*. 2021; Kumar *et al*. 2020). HSPs are controlled by the action of diverse heat shock factors which are activated under stress conditions (Maaroufi & Tanguay 2013; Jacob *et al.* 2017).

By definition, protein denaturation is a constant direct or indirect consequence of any stress, as stresses are defined as factors limiting normal cellular functions carried out by proteins (Atkinson & Urwin 2012). Potentially, any stressor that induces protein misfolding would require HSPs. Thereby, chaperones are considered as powerful buffers against protein misfolding during environmental stress (including drought) and consequent genetic variations (Carey *et al.* 2006; Maaroufi & Tanguay 2013). The importance of HSPs is not limited to heat stress management, but these molecules are also involved in other stresses, such as cold, osmoses, drought, salt, UV, high light, oxidative stress, and pathogen infection (Swindell *et al.* 2007; Maaroufi & Tanguay 2013; Di Donato & Geisler 2019; Kumar *et al*. 2020; Guo *et al*. 2021).

The main inducers of chaperones are heat-shock factors (HSFs) and the diversity of the HSFs family in plants causes their study difficult. However, sequence and expression pattern comparisons showed both distinct and overlapping functions in stress resistance and development. The amount of free HSPs is the sensor of the cell capacity to maintain a stable proteome and feeds back on its own production. Indeed, in unstressed tissues, the commonly accepted "chaperone titration model" specifies that HSFs are sequestered by HSP70/90 and maybe other chaperones (Jacob *et al.* 2017). The HSP90 chaperone machinery controls multiple cellular processes by regulating the maturation, stability, activity, and turnover of its substrates, the so-called client proteins (Di Donato & Geisler 2019).

119 DnaJ (HSP40) proteins (TaDnaJs; encoded by 313 genes) and 41 HSP70 proteins (TaHsp70s; encoded by 95 genes) have been identified and classified in wheat into six and four groups, respectively, via a phylogenetic analysis. An examination of protein sequence alignment revealed diversity in the TaDnaJ structural organization, but a highly conserved J-domain characterized by an HPD motif followed by DRD or DED motifs was observed (Guo *et al*. 2021). In the work of Kumar *et al*. (2020) using Position-Specific Scoring Matrix (PSSMs) and by sequence homology 753 *TaHSPs* including 169 *TaSHSP* (small HSP), 273 *TaHSP40*, 95 *TaHSP60*, 114 *TaHSP70*, 18 *TaHSP90*, and 84 *TaHSP100* were identified in the wheat genome. Compared with other grass species, the number of HSPs in wheat is relatively high probably due to the higher ploidy level and a large number of tandem duplication was identified in *TaHSPs*, especially *TaSHSPs*. The *TaHSPs* genes show random distribution on chromosomes, however, there are more *TaHSPs* in B and D sub-genomes as compared to the A sub-genome (Kumar *et al*. 2020).

Information about the involvement of HSPs in drought stress signalling is rare, however high expression of *TaSHSP* was observed during seed development, especially during the grain filling stage (Kumar *et al*. 2020). It was found that both the overexpression of HSC70 and the use of a dominant-negative form of HSP90 disrupt ABA-mediated stomata closure, thereby negatively affect water loss in stress conditions (Di Donato & Geisler 2019). The impact of ABA treatment on HSC70, HSP90, SGT1 (co-chaperone of HSP90, suppressor of G-two allele of *Skp1*), and RAR1 (co-chaperone of HSP90, required for *Mla12* powdery mildew resistance) was investigated by quantitative polymerase chain reaction (qPCR). A decrease in SGT1a mRNA and an increase in HSC70-4 mRNA was observed. HSC70-1 and HSC70-4 must therefore share the same function regarding the regulation of ABA signalling under physiological conditions. Only HSC70-4 is involved in mitigating ABA signals (Clement *et al.* 2011).

3.3 Dehydrins activation in cereals during drought

Dehydrins are significantly disordered proteins which are produced under water stress conditions. They play an essential role in the response of plants to abiotic stress and in adapting them to the stress conditions (Kosová *et al.* 2013; Thomas 2015). Their higher accumulation is usually induced in vegetative plant tissues under various stress factors that cause cell dehydration including salinity, lack of water, cold, and frost (Kosová *et al.* 2013). Several physiological studies oriented in plant response to stress have shown a positive relationship between the level of accumulation of transcripts or dehydrin proteins and plant tolerance to stress, especially in wheat and barley (*Hordeum vulgare* L.) (Kosová *et al.* 2013; Vítámvás *et al.* 2019).

The structural physicochemical and functional characterization of plant dehydrins and how their properties can be used to improve resistance to stress in plants has been described (Hanin *et al.* 2011). Dehydrins can non-specifically bind proteins and membranes contributing to the protection of their functions and structure from damage caused by environmental stresses. Dehydrins can also bind the DNA and act by not only protecting but also repairing the molecule under the attack of environmental stress factors (Liu *et al.* 2017).

Drought induces cell dehydration and expression of several dehydrins in wheat and barley. In durum wheat, the accumulation of YSK2 dehydrin DHN5 was studied in two cultivars exposed to drought stress. A different pattern of phosphorylation was observed in both studied cultivars, where the drought-tolerant cultivar reveals higher ranges of phosphorylation than the sensitive one (Kosová *et al.* 2014). Phosphorylation is associated with the different subcellular localization of the protein affecting the final function of the protein (Kosová *et al.* 2014). Quantitative and qualitative differences in low molecular weight dehydrin proteins were found in two barley cultivars with different drought tolerance capacity when plants were exposed to reduced field water capacity (Škodáček & Prášil 2011).

Qualitative differences in accumulated dehydrin proteins may be due to either the accumulation of different low molecular weight *Dhn* genes or allelic variants of the same genes, which differ in copy number of hydrophilic Φ segments and electrophoretic mobility, as it was described for *Dhn4* (Kosová *et al.* 2014). The authors report that the gene expression is an indicator of drought stress and an appropriate adaptation mechanism and the demonstration of drought stress increases with the exposure time during the vegetative period and during the critical phases of plant development (Kosová *et al.* 2014; Klimešová *et al.* 2017).

3.4 Importance of antioxidants in plant protection against drought

In wheat, several studies have reported changes in the activity of many enzymes of the antioxidant defence system to control oxidative stress induced by environmental stresses. The enzymatic components comprise several antioxidant enzymes, such as superoxide dismutase, catalase, glutathione peroxidase, guaiacol peroxidase, peroxiredoxins, and enzymes of the ascorbate-glutathione cycle, such as ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase (Caverzan *et al.* 2016; Prasad *et al.* 2017; Jiang *et al.* 2019; Kapoor *et al.* 2020). Non-enzymatic components include the major cellular redox buffers ascorbate and glutathione as well as tocopherols, carotenoids, and phenolic compounds. Alterations in the activity of superoxide dismutase, ascorbate peroxidase, catalase, glutathione reductase, and guaiacol peroxidase and in the reactive oxygen species (ROS) concentration were reported in wheat plants in a field and at laboratory conditions (Caverzan *et al.* 2016; Cheng *et al.* 2016; Jiang *et al.* 2019). Furthermore, many reports demonstrate that the effect of abiotic stress in wheat is genotype-specific, where some genotypes show different responses in the same stress condition. Drought-tolerant genotypes generally maintained a higher antioxidant capacity resulting in lower oxidative damage (Devi *et al.* 2012; Caverzan *et al.* 2016). Wheat responses also depend on the tissue type, length, and intensity of the stress as well as on the developmental stage proving the complexity of the mechanisms of production and detoxification of ROS and the effect of ROS on antioxidant systems. Many studies have reported an increase in the concentration of H_2O_2 after exposure to a stress and its production dependents on the intensity and duration of the stress factor (Alexieva *et al.* 2001; Caverzan

et al. 2016; Jiang *et al.* 2019).

Furthermore, the H_2O_2 level differs between various cellular compartments and is related to the type of stress (Caverzan *et al.* 2016; Dikilitas *et al.* 2020). The observed increase in enzymatic activities and decrease in oxidative damage are closely related. The expression of many antioxidant enzymes is positively correlated with higher tolerance levels against abiotic stresses. The activation of some enzymes leads to plant protection against oxidative damage. In rice plants, an important cereal model, increased concentration of antioxidant enzymes and increased expression levels of related genes have been connected with the plant response to drought (Caverzan *et al.* 2016).

Superoxide dismutases (SODs) are a family of key antioxidant enzymes that play a crucial role in plant growth and development and are regulated by development, tissue- type, and environmental signals (Jiang *et al.* 2019). In drought stress, SODs represent a frontline in the defence against ROS, they catalyse the dismutation of $O_2^{\cdot}$ (superoxide radical) to H_2O_2 (Gill *et al*. 2015). Catalases (CATs) are abundantly, but not exclusively, localized in peroxisomes and their function is to remove the H_2O_2 by reducing H_2O_2 to two molecules of H_2O. Drought-induced H_2O_2 accumulation is in a correlation with decreases in soil water content and CO_2 assimilation. Leaf H_2O_2 content increases even though total CAT activity doubling under severe drought conditions. Drought decreases abundance and modifies the pattern, of *CAT1* and *CAT2* mRNAs. The abundance of *CAT1* transcripts is regulated by circadian controls that persist in continuous darkness, while *CAT2* is modulated by light (Luna *et al*. 2005).

In wheat, a mutant line with reduced thylakoid ascorbate peroxidases (APXs) activity leads to regress in photosynthesis (Danna *et al.* 2003). Rice mutants double silenced for cytosolic APXs exhibit high guaiacol peroxidase activity, which can contribute to the cytosolic H_2O_2 scavenging in the vacuoles or apoplasts (Bonifacio *et al.* 2011). APXs catalyse the conversion of H_2O_2 into H_2O and use ascorbate as a specific electron donor. APXs proteins are distributed in chloroplasts, mitochondria, peroxisomes, and cytosol. The APXs genes show different modulation by several abiotic stresses in plants. The balance between SODs, CATs, and APXs is important for determining the intracellular level of ROS, besides changes in the balance of these appear to induce compensatory mechanisms.

The expression of wheat glutathione peroxidase (GPX) genes was altered when wheat plants were exposed to salt, H_2O_2, and ABA treatment. Moreover, other findings suggest that GPX not only acts as scavengers of H_2O_2 to control abiotic stress responses but also plays important roles in salt and ABA-signalling cascades (Zhai *et al.* 2013). In plants, the GPX proteins are distributed in mitochondria, chloroplasts, and the cytosol (Caverzan *et al.* 2016).

ROS are well recognized for playing a dual role, both as malignant as well as beneficial, depending on their concentration in the plant. The role of ROS as signalling molecules includes also processes related to growth, cell cycle, development, senescence, programmed cell death, stomatal conductance, and hormonal signalling (Inze *et al.* 2012; Caverzan *et al.* 2016). H_2O_2 is considered a signalling molecule in plants that mediates responses to various biotic and abiotic stresses. The biological effect of H_2O_2 is related to several factors, such as the site of production, the developmental stage of the plant, and its concentration (Wahid *et al.* 2007; Petrov & Breusegem 2012). Thus, due to the property that in low concentrations the H_2O_2 acts as a stress signal, many studies have demonstrated that its application can induce stress tolerance in plants (e.g., He *et al.* 2009; Caverzan *et al.* 2016; Jiang *et al.* 2019; Dikilitas *et al*. 2020). Low H_2O_2 treatments improve seed germination, seedling growth, and resistance to abiotic stresses (Caverzan *et al.* 2016). In wheat, it was observed that seed pre-treatment with H_2O_2 enhances the drought tolerance of seedlings (He *et al.* 2009). The exogenous H_2O_2 treatment also protects wheat seedlings from damage by salt stress and seeds pre-treatment enhances salt tolerance of wheat seedlings and decreases oxidative damage (Wahid *et al.* 2007). In rice plants, H_2O_2 not only acts as a toxic molecule, but also as a signalling molecule associated with salinity, cadmium, and ABA stresses (Kao 2014). In wheat, H_2O_2 plays an important role as a signal molecule, but also as a harmful chemical (Ge *et al.* 2013; Dikilitas *et al.* 2020).

Metabolic analyses at the level of phenolics showed an increase in the free and bound fraction

of phenolic acids almost exclusively in the shoots, and flavonoid isoorientin increased considerably as a protective action against oxidative stress (Gregorová *et al.* 2015).

4. BIOCHEMICAL RESPONSES TO DROUGHT IN CEREALS

During drought stress, plant cells accumulate soluble substances, contributing to a higher viscosity in the cytoplasm. The content of these special substances may become toxic under certain conditions and may cause problems in the formation of enzymes and the whole process of photosynthesis (Danna *et al.* 2003; Han *et al.* 2015). In a short-term drought, Rubisco is relatively stable and it decomposes just after a few days. Fixed-binding inhibitors may reduce the activity of the Rubisco within 24 hours. The rapid decrease in "dry" photosynthesis is accompanied by a reduction in the maximum rate of ribulose-1,5-carboxylate, the rate of regeneration of ribulose-1,5-bisphosphate, Rubisco, phosphoenolpyruvate carboxylase, NADP-malic enzyme, fructose-1,6-bisphosphatase, and orthophosphate-dikinase pyruvate (Reddy *et al.* 2004; Zhou *et al.* 2007). In addition, noncyclic electron transport is reduced to meet the requirements for reduced NADPH production, thereby reducing ATP and ROS synthesis (Reddy *et al.* 2004).

Different cultivars within crop species may strongly differ in their response and adaptation to drought stress (Abid *et al.* 2018). Studies at the transcriptomic level have revealed that the drought-tolerant and sensitive wheat genotypes can adopt different molecular strategies to overcome with drought stress. One of the main differences is the differential expression of some drought-inducible genes for cell protection (e.g., antioxidants, detoxifiers, dehydrins, transporters, and compatible solutes), regulation (e.g., kinases, transcription factors, and hormones), and remodelling of cellular components (e.g., membrane systems, cell wall, and primary metabolic networks). A large number of these genes are often activated in drought-sensitive wheat genotype, while a tolerant genotype shows a constitutive expression of several genes activated in a sensitive genotype and that contribute to limiting drought effects and perception. In addition, signal transduction and hormone-dependent regulation pathways are also different in various wheat genotypes. The drought-tolerant genotype can quickly sense drought and trigger the signal transduction pathways for activation of downstream elements for survival from drought stress (Cheng *et al.* 2016).

5. MOLECULAR TOOLS FOR IMPROVEMENT OF DROUGHT TOLERANCE IN CEREALS

Drought tolerance is not a qualitative trait, but a complex of quantitative plant traits controlled by numerous genes and other plant traits with minor individual effects (Senapati *et al.* 2018). In recent years, knowledge about molecular regulation has been generated to understand drought stress responses. For example, information obtained by transcriptome analysis has enhanced our knowledge and facilitated the identification of candidate genes that can be utilized for plant breeding. On the other hand, it becomes more evident that the translational and post-translational machinery plays a major role in stress adaptation, especially for immediate molecular processes during stress adaptation. Therefore, it is essential to measure protein levels and post-translational protein modifications to reveal information about stress-inducible signal perception and transduction, translational activity, and induced protein levels (Ghatak *et al.* 2017). Research in transcriptomics, proteomics, and metabolomics is increased to understand the mechanisms of drought tolerance in plants (Swindell *et al.* 2007).

Proteomics has become the most direct and powerful tool to obtain protein expression information of plants responses to drought stress, thereby complementing transcriptomic studies. Comparative proteomics of drought-tolerant and sensitive wheat genotypes is a strategy to understand the complexity of molecular mechanism in wheat in response to drought stress (Cheng *et al.* 2016). Dehydrins have been reported as important factors in stress tolerance and the genetic locations of some dehydrin family members co-locate with QTL for drought tolerance in barley (Thomas 2015). Of the antioxidant components, *TaSOD* genes are involved in the regulation

of wheat tissue development and likely play important role in response to abiotic stress including a longer duration of drought. Four of these genes (*TaSOD1.1a*, *TaSOD1.4*, *TaSOD2.1*, and *TaSOD2.3*) showed up-regulation in leaf and five genes (*TaSOD1.7*, *TaSOD1.9*, *TaSOD1.11a*, *TaSOD2.1*, and *TaSOD2.3*) showed up-regulation in the root (Jiang *et al.* 2019).

Efforts to improve crops tolerance to drought and associated soil salinity are considerable, especially in the context of climatic change and irrigation water scarcity. Using the combination of DNA fingerprints of different genotypes with phenotypic measurements, specific chromosomal regions – so-called quantitative trait loci (QTL) – were associated with the expressed traits. Specific DNA markers have been linked with favourable QTLs using the technology of marker-assisted selection (MAS) (Tuberosa & Salvi 2006). Thanks to the advances in next-generation sequencing, the identification of major QTLs regulating specific drought responses is successful and via the development of large numbers of genetic markers such as single nucleotide polymorphisms (SNPs) and insertion-deletions (InDels) it represents an efficient way to improve drought tolerance in cereal crops (Kole *et al.* 2015). Studies reporting major drought-responsive genes and QTLs in wheat have recently been published (Choudhary *et al.* 2019; Khadka *et al.* 2020; Pang *et al.* 2020) suggesting that for the past decade, QTL has been the focal target of research to identify the genetic loci regulating the adaptive response of crops to drought stress (Zenda *et al.* 2020).

In addition to the classical and molecular plant breeding techniques, the key tool became the transfer of genes and gene regulatory regions related to plant water management. Transgenic approaches using candidate genes such as transcription factors, microRNAs, as well as genome editing technology have been well summarized (Tuberosa & Salvi 2006; Abdallah *et al*. 2015; Paul & Roychoudhury 2018; Jha 2019; Anwar & Kim 2020). Attractive targets of plant genetic engineering for drought tolerance are considered transcription factors (e.g. WRKY, MYB, NAC, AP2/ERF, GBF3). Their potential in the engineering of stress-tolerant monocot plants has been already reviewed (e.g., Javed *et al*. 2020). The subjects of interest are also signal molecules and genes encoding them to help the plants to cope with abiotic stresses (Ahmed *et al*. 2020). Many genes participating in drought stress response have been already identified and transferred into cultured plants, including the most important cereals. Transgenic wheat, barley, maize, rice, and other cereals with increased water use efficiency and drought tolerance were experimentally developed (Gao *et al*. 2005; Napolean *et al*. 2018; Zhou *et al*. 2018; González *et al*. 2019; Khan *et al*. 2019; Oladosu *et al*. 2019). However, an only a very limited number of drought-tolerant cereal cultivars created by genetic transformation are so far registered for commercial use. The most important databases of approved genetically modified plants managed by the International Service for the Acquisition of Agri-Biotech Applications (ISAAA's GM Approval Database, http://www.isaaa.org/gmapprovaldatabase/) and the European Community register of GM food and feed (https://ec.europa.eu/food/plant/gmo/eu_register_en) include at present time only drought tolerant genetically modified maize, sugarcane, and soybean. Drought tolerance of maize was obtained by the introduction of the gene *cspB* that encodes the cold shock protein B. The *cspB* transgene maintains normal cellular functions under water stress conditions in the plant by preserving RNA stability and translation.

Another co-solution of abiotic stress problem in plants is a better understanding of interactions between plants and plant growth-promoting microorganisms (PGPM). They can protect plants from the negative effects of drought and salinity (Khan *et al*. 2020; Ma *et al*. 2020). Biotechnology and gene transfer technologies could increase the effectiveness of plant-microorganism interactions. Genetically engineered PGPM enhance the survival of plants under water deficiency as it has already been proven in plants colonized by genetic engineered soil bacteria over-producing trehalose (Vílchez *et al*. 2016).

Biotechnology tools and genetic engineering approaches, along with a better understanding of plants, and other stress mitigation strategies, are solutions for the very near future crop production with limited water resources.

6. CONCLUSIONS

Plant responses to stress are dynamic processes, which are able to enhance tolerance/resistance mechanisms and establish metabolic homoeostasis under extreme environmental conditions. Regulatory proteins play an important role in regulating the alterations under water deficit conditions and represent some of the most important targets for crop improvement. Protein phosphorylation plays an important role in signal perception and transduction under drought stress. Several kinases and phosphatases, and other signalling proteins are regulated leading to stress adaptation and possible tolerance mechanisms like stomata closure. Stress acclimatization is an energy-consuming process which is indicated by alterations in energy metabolism. Therefore, increased abundance of the enzymes involved in glycolysis is during drought observed. Drought stress leads to an enhanced risk of protein damage due to cellular instability/imbalances. Therefore, several proteins with protective mechanisms show increased levels (for example HSPs, namely HSP70, HSP90). Disturbed cellular metabolism leads to oxidative damage and hence increase in ROS scavenging enzymes was also observed (SOD, GST, CAT, APX, and others) which is one of the common and practical features in plants under drought stress.

Sustainable crop production is the major challenge in the current global climate change scenario. Drought stress is one of the most critical abiotic factors which negatively impact crop productivity. Cereals are the major food crops that are necessary for the survival of the entire human population across the globe. Not only humans but also livestock farming depend on these crops. Considering all the drastic global climatic changes, our food security and its distribution is a big question. Marker-Assisted Breeding and SMART Breeding Techniques are key in agricultural productivity. Proteomics is one such tool to improve SMART breeding. The integration of genomics, proteomics, transcriptomics, and metabolomics is important for future research in green systems biology to improve its application in cereal crops. Increasing the resistance of wheat to drought and drought-related stresses is one of the most important objectives of breeding programs. However, from the point of view of current use in plant production, the greatest advances in the development of plants tolerant of drought and other abiotic stresses have been made through genetic engineering technologies.

Acknowledgements: This work was supported by the Slovak Research and Development Agency (projects APVV-18-0154 and APVV-17-0113) and and by the Operational Programme Integrated Infrastructure within the project: Sustainable smart farming systems taking into account the future challenges 313011W112, cofinanced by the European Regional Development Fund.

7. REFERENCES

Abdallah, N.A., Prakash, C.S. and Mchughen A.G. 2015. Genome editing for crop improvement: Challenges and opportunities. *GM Crops & Foods*, *6*, 183 – 205. DOI: 10.1080/21645698.2015.1129937.

Abid, M., Ali, S., Qi, L.K., Zahoor, R., Tian, Z., Jiang, D., Snider, J.L. and Dai, T. 2018. Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). *Scientific Reports*, *4615*(8), 1 – 15. DOI:10.1038/s41598-018-21441-7.

Abobatta, W.F. 2019. Drought adaptive mechanisms of plants – a review. *Advances in Agriculture and Environmental Science*, *2*(1), 62 – 65. DOI:10.30881/aaeoa.00022.

Ahmed, R.F., Irfan, M., Shakir, H.A., Khan, M. and Chen, L. 2020. Engineering drought tolerance in plants by modification of transcription and signalling factors. *Biotechnology & Biotechnological Equipment*, *34*, 781 – 789. DOI: 10.1080/13102818.2020.1805359.

Alghabari, F. and Ihsan, M.Z. 2018. Effects of drought stress on growth, grain filling duration, yield and quality attributes of barley (*Hordeum vulgare* L.). *Bangladesh Journal of Botany*, *47*(3), 421 – 428. DOI:10.3329/bjb.v47i3.38679.

Alghabari, F., Ihsan, M.Z., Hussain, S., Aishia, G., Daur, I. 2015. Effect of Rht alleles on wheat grain yield and quality under high temperature and drought stress during booting and anthesis. *Environmental Science and Pollution Research*, *22*(1), 15506 – 15515. DOI:10.1007/s11356-015-4724-z.

Andersen, M.N., Asch, F., Wu, Y., Jensen, Ch.R., Næsted, H., Mogensen, V.O. and Koch, K.E. 2002. Soluble invertase expression is an early target of drought stress during the critical, abortion-sensitive phase of young ovary development in maize. *Plant Physiology*, *130*(2), 591 – 604. DOI:10.1104/pp.005637.

Anjum, S.A., Xie, X., Wang, L., Saleem, M.F., Man, C. and Lei, W. 2011. Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research, 6*(9), 2026 – 2032. DOI:10.5897/AJAR10.027.

Araus, J.L., Slafer, G.A., Reynolds, M.P. and Royo, C. 2002. Plan breeding and drought in C_3 cereals: What should we breed for? *Annals of Botany*, *89*, 925 – 940. DOI:10.1093/aob/mcf049.

Atkinson, N.J. and Urwin, P.E. 2012. The interaction of plant biotic and abiotic stresses: from genes to the field. *Journal*

of Experimental Botany, *63*(10), 3523 – 3543. DOI:10.1093/jxb/ers100.

Anwar, A. and Kim, J.-K. 2020. Transgenic breeding approaches for improving abiotic stress tolerance: Recent progress and future perspectives. *International Journal of Molecular Sciences*, *21*, 2695. DOI:10.3390/ijms21082695.

Bonifacio, A., Martins, M.O., Ribeiro, C.W., Fontenele, A.V., Carvalho, F.E.L., Margis-Pinheiro, M., Silveira, J.A.G. 2011. Role of peroxidases in the compensation of cytosolic ascorbate peroxidase knockdown in rice plants under abiotic stress. *Plant, Cell & Environment*, *34*(10), 1705 – 1722. DOI:10.1111/j.1365-3040.2011.02366.x.

Carey, C.C., Gorman, C.F. and Rutherford, S. 2006. Modularity and intrinsic evolvability of Hsp90-buffered change. *PLOS ONE*, *1*(1), 1 – 6. DOI:10.1371/journal.pone.0000076.

Caverzan, A., Casassola, A. and Brammer, S.P. 2016. Antioxidant responses of wheat plants under stress. *Genetics and Molecular Biology*, *39*(1), 1 – 6. DOI:10.1590/1678-4685-GMB-2015-0109.

Cheng, L., Wang, Y., He, Q., Li, H., Zhang, X. and Zhang, F. 2016. Comparative proteomics illustrates the complexity of drought resistance mechanisms in two wheat *Triticum aestivum* L.) cultivars under dehydration and rehydration. *BMC Plant Biology*, *16*(1), 1 – 23. DOI:10.1186/s12870-016-0871-8.

Choudhary, M., Wani, S.H., Kumar, P., Bagaria, P.K., Rakshit, S., Roorkiwal, M. and Varshney, R.K. 2019. QTLian breeding for climate resilience in cereals: progress and prospects. *Functional & Integrative Genomics*, *19*, 685 – 701. DOI: 10.1007/s10142-019-00684-1.

Danna, C.H., Bartoli, C.G., Sacco, F., Ingala, L.R., Santa-María, G.E., Guiamet, J.J. and Ugalde, R.A. 2003. Thylakoid-bound ascorbate peroxidase mutant exhibits impaired electron transport and photosynthetic activity. *Plant Physiology*, *132*(4), 2116 – 2125. DOI:10.1104/pp.103.021717.

Davies, W.J., Kudoyarova, G. and Hartung, W. 2005. Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant´s response to drought. *Journal of Plant Growth Regulation*, *24*, 285 – 295. DOI:10.1007/s00344-005-0103-1.

Daszkowska-Golec, A. and Szarejko, I. 2013. *Abiotic Stress - Plant responses and applications in agriculture: The molecular basis of ABA-mediated plant response to drought.* Rijeka: InTech, 418 pp. ISBN 978-953-51-1024-8.

Di Donato, M.D. and Geisler, M. 2019. HSP90 and co-chaperones: a multitaskers' view on plant hormone biology. *FEBS Letters*, *593*(13), 1415 – 1430. DOI:10.1002/1873-3468.13499.

Dikilitas, M., Simsek, E. and Roychoudhury, A. 2020. Modulation of abiotic stress tolerance through hydrogen peroxide. Chapter 7. *Protective Chemical Agents in the Amelioration of Plant Abiotic Stress,* 147 – 173. USA: John Wiley & Sons, Ltd. DOI:10.1002/9781119552154.ch7.

Dolferus, R., Ji, X. and Richards, R.A. 2011. Abiotic stress and control of grain number in cereals. *Plant Science*, *181*(4), 331 – 341. DOI:10.1016/j.plantsci.2011.05.015.

Earl, H.J. and Davis, R.F. 2003. Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize. *Agronomy Journal*, *95*(3), 688 – 696. DOI:10.2134/agronj2003.0688.

FAO. 2013. *Statistical yearbook 2013*. Rome: Food and Agriculture Organization of the United Nations, 307 pp. ISBN 978-92-5-107396-4.

FAO. 2018. *The impact of disasters and crises on agriculture and food security*. Rome: Food and Agriculture Organization of the United Nations, 168 pp. ISBN: 978-92-5-130359-7

Farooq, M, Wahid, A., Kobayashi, N., Fujita, D. and Basra, S.M.A. 2009. Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development, 29*(1), 185 – 212. DOI:10.1051/agro:2008021.

Fedoroff, N., Battisti, D.S., Beachy, R.N., Cooper, P.J.M., Fischhoff, D.A., Hodges, C.N., Knauf, V.C., Lobell, D., Mazur, B.J., Molden, D., Reynolds, M.P., Ronald, P.C., Rosegrant, M.W., Sanchez, P.A., Vonshak, A. and Zhu, J-K. 2010. Radically rethinking agriculture for the 21st century. *Science*, *327*(5967), 833 – 834. DOI:10.1126/science.1186834.

Gao, S., Xu, H., Cheng, X., Chen, M., Xu, Z., Li, L., Ye, X., Du, L., Hao, X. and Ma, Y. 2005. Improvement of wheat drought and salt tolerance by expression of a stress inducible transcription factor GmDREB of soybean (*Glycine max*). *Chinese Science Bulletin*, *50*, 2714 – 2723. DOI: 10.1007/BF02899641.

Garg, B.K. 2003. Nutrient uptake and management under drought: nutrient-moisture interaction. *Current Agriculture*, *27*(1/2), 1 – 8.

Ge, P., Hao, P., Cao, M., Guo, G., Lv, D., Subburaj, S., Li, X., Yan, X., Xiao, J., Ma, W. and Yan, Y. 2013. iTRAQ-based quantitative proteomic analysis reveals new metabolic pathways of wheat seedling growth under hydrogen peroxide stress. *Proteomics*, *13*(20), 3046 – 3058. DOI:10.1002/pmic.201300042.

Ghatak, A., Chaturvedi, P. and Weckwerth, W. 2017. Cereal crop proteomics: systemic analysis of crop drought stress responses towards marker-assisted selection breeding. *Frontiers in Plant Science*, *8*(757), 1 – 25. DOI:10.3389/fpls.2017.00757.

Gill, S.S., Anjum, N.A., Gill, R., Yadav, S., Hasanuzzaman, M., Fujita, M., Mishra, P., Sabat, S.C. and Tuteja, N. 2015. Superoxide dismutase – Mentor of abiotic stress tolerance in crop plants. *Environmental Science and Pollution Research*, 22, 10375 – 10394. DOI:10.1007/s11356-015-4532-5.

González, F.F., Capella, M., Ribichich, K.K., Curífn, F., Giacomelli, J.J., Ayala, F., Watson, G., Otegui, M.E. and Chan, R.L. 2019. Field-grown transgenic wheat expressing the sunflower gene *HaHB4* significantly outyields the wild type. *Journal of Experimental Botany*, *70*, 1669 – 1681. DOI:10.1093/jxb/erz037.

Gregorová, Z., Kováčik, J., Klejdus, B., Maglovski, M., Kuna, R., Hauptvogel, P. and Matušíková, I. 2015. Drought – induced responses of physiology, metabolites, and PR proteins in *Triticum aestivum*. *Journal of Agricultural and Food Chemistry*, *63*(37), 8125 – 8133. DOI:10.1021/acs.jafc.5b02951.

Guo, H., Zhang, H., Wang, G., Wang, Ch., Wang, Y., Liu, X. and Ji, W. 2021. Identification and expression analyses of heat-shock proteins in wheat infected with powdery mildew and stripe rust. *The Plant Genome*, *e20092*, 1 – 15. DOI:10.1002/tpg2.20092

Hamim, 2005. Photosynthesis of C3 and C4 species in response to increased CO2 concentration and drought stress. *Hayati*, *12*(4), 131 – 138.

Han, H., Tian, Z., Fan, Y., Cui, Y., Cai, J., Jiang, D., Cao, W. and Dai, T. 2015. Water-deficit treatment followed by re-watering stimulates seminal root growth associated with hormone balance and photosynthesis in wheat (*Triticum aestivum* L.) seedlings. *Plant Growth Regulation*, *77*(2), 201 – 210. DOI: 10.1007/s10725-015-0053-y.

Hanin, M., Brini, F., Ebel, Ch., Toda, Y., Takeda, S. and Masmoudi, K. 2011. Plant dehydrins and stress tolerance: versatile proteins for complex mechanisms. *Plant Signaling & Behavior*, *6*(10), 1503 – 1509. DOI:10.4161/psb.6.10.17088.

Houshmand, S., Arzani, A. and Mirmohammadi-Maibody,

S.A.M. 2014. Effects of salinity and drought stress on grain quality of durum wheat. *Communications in Soil Science and Plant Analysis*, *45*(3), 297–308. DOI: 10.1080/00103624.2013.861911.

Izanloo, A., Condon, A.G., Langridge, P., Tester, M. and Schnurbusch, T. 2008. Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. *Journal of Experimental Botany*, *59*(12), 3327–3346. DOI:10.1093/jxb/ern199.

Jacob, P., Hirt, H. and Bendahmane, A. 2017. The heat-shock protein/chaperone network and multiple stress resistance. *Plant Biotechnology Journal*, *15*(4), 405–414. DOI: 10.1111/pbi.12659.

Jansen, G., Schliephake, E., Kopahnke, D. and Ordon, F. 2013. Effect of N-fertilization, fungicide treatment, seed density and abiotic stress factors on the total ß-glucan content of six-rowed winter barley (*Hordeum vulgare* L.). *Journal of Applied Botany and Food Quality*, *86*(1), 180–184. DOI: 10.5073/JABFQ.2013.086.024.

Javed, T., Shabbir, R., Ali, A., Afzal, I., Zaheer, U. and Gao, S.-J. 2020. Transcription factors in plant stress responses: Challenges and potential for sugarcane improvement. *Plants*, *9*, 491. DOI:10.3390/plants9040491.

Jha, S. 2019. Transgenic approaches for enhancement of salinity stress tolerance in plants. In Singh, S.P., Upadhyay, S.K., Pandey, A., Kumar, S. (Eds.) *Molecular Approaches in Plant Biology and Environmental Challenges, Energy, Environment, and Sustainability*. Singapore: Springer Nature, 266–322. ISBN 978-981-15-0692-5

Jiang, W., Yang, L., Yiqin, H., Zhang, H., Li, W., Chen, H., Ma, D. and Yin, J. 2019. Genome-wide identification and transcriptional expression analysis of superoxide dismutase (SOD) family in wheat (*Triticum aestivum*). *Peer J*, *19*(7), 1–26. DOI:10.7717/peerj.8062.

Kao, CH. 2014. Role of hydrogen peroxide in rice plants. *Crop, Environment & Bioinformatics*, *11*(3), 1–10. DOI:20.1093/jxb/ert375.

Kapoor, D., Bhardwaj, S., Landi, M., Sharma, A., Ramakrishnan, M. and Sharma, A. 2020. The Impact of drought in plant metabolism: How to exploit tolerance mechanisms to increase crop production. *Applied Sciences*, *10*(16), 1–19. DOI:10.3390/app10165692.

Khadka, K., Earl, H.J., Raizada, M.N. and Navabi, A. 2020. A physio-morphological trait-based approach for breeding drought tolerant wheat. *Frontiers in Plant Science*, *11*, article: 715. DOI:10.3389/FPLS.2020.00715.

Khan, N., Ali, S., Tariq, H., Latif, S., Yasmin, H., Mehmood, A. and Shahid, M.A. 2020. Water conservation and plant survival strategies of Rhizobacteria under drought stress. *Agronomy*, *10*, 1683. DOI:10.3390/agronomy10111683.

Khan, S., Anwar, S., Yu, S., Sun, M., Yang, Z. and Gao, Z.-Q. 2019. Development of drought-tolerant transgenic wheat: Achievements and limitations. *International Journal of Molecular Sciences*, *20*, 3350. DOI:10.3390/ijms20133350.

Klimešová, J., Holková, L. and Středa, T. 2017. The expression of dehydrin genes and the intensity of transpiration in drought-stressed maize plants. *Cereal Research Communications*, *45*(3), 355–368. DOI:10.1556/0806.45.2017.017.

Kole, C., Muthamilarasan, M., Henry, R. *et al.* 2015. Application of genomics-assisted breeding for generation of climate resilient crops: progress and prospects. *Frontiers in Plant Science*, *6*, article: 563. DOI:10.3389/fpls.2015.00563 .

Kumar, A., Sharma, S., Chunduri, V. *et al.* Genome-wide identification and characterization of heat shock protein family reveals role in development and stress conditions in *Triticum aestivum* L. *Scientific Reports, 10*(7858). DOI:10.1038/s41598-020-64746-2.

Lamaoui, M., Jemo, M., Datla, R. and Bekkaoui, F. 2018. Heat and drought stresses in crops and approaches for their mitigation. *Frontiers in Chemistry*, *6*, article: 26. DOI:10.3389/fchem.2018.00026.

Li, Y.F., Wu, Y., Hernandez-Espinosa, N. and Peña, R.J. 2013. Heat and drought stress on durum wheat: Responses of genotypes, yield and quality parameters. *Journal of Cereal Science*, *57*(3), 398–404. DOI:10.1016/j.jcs.2013.01.005.

Luna, C.M., Pastori, G.M., Driscoll, S., Groten, K., Bernard, S. and Foyer, Ch.H. 2005. Drought controls on H_2O_2 accumulation, catalase (CAT) activity and CAT gene expression in wheat. *Journal of Experimental Botany*, *56*(411), 417–423. DOI:10.1093/jxb/eri039.

Magallanes-López, A.M., Ammar, K., Morales-Dorantes, A., González-Santoyo, H., Crossa, C. and Guzmán, C. 2017. Grain quality traits of commercial durum wheat varieties and their relationships with drought stress and glutenins composition. *Journal of Cereal Science*, *75*(1), 1–9. DOI: 10.1016/j.jcs.2017.03.005.

Mitra, J. 2001. Genetics and genetic improvement of drought resistance in crop plants. *Current Science*, *80*(6), 758–763.

Napolean, T., Kaul, J., Mukri, G. and Mittal, S. 2018. Genomics-enabled next-generation breeding approaches for developing system-specific drought tolerant hybrid in maize. In Luo, L., Mei, H., Tuberosa, R., Nguyen, H.T. and Lu, B. (Eds.) *Crop Breeding for Drought Resistance*. Lausanne: Frontiers Media, pp. 200–221. DOI:10.3389/fpls.2018.00361.

Ni, Z., Li, H., Zhao, Y., Peng, H., Hu, Z., Xin, M. and Sun, Q. 2018. Genetic improvement of heat tolerance in wheat: Recent progress in understanding the underlying molecular mechanisms. *The Crop Journal*, *6*(1), 32–41. DOI: 10.1016/j.cj.2017.09.005.

Nuttall, J.G., O'leary, G.J., Panozzo, J.F., Walker, C.K., Barlow, K.M. and Fitzgerald, G.J. 2017. Models of grain quality in wheat – a review. *Field Crops Research*, *202*(12), 136–145. DOI:10.1016/j.fcr.2015.12.011.

Oladosu, Y., Rafii, M.Y., Samuel, C., Fatai, A., Magaji, U., Kareem, I., Kamarudin, Z.S., Muhammad, I. and Kolapo, K. 2019. Drought resistance in rice from conventional to molecular breeding: A review. *International Journal of Molecular Sciences*, *20*, 3519. DOI:10.3390/ijms20143519.

Osakabe, Y., Osakabe, K., Shinozaki, K. and Tran, L.S.P. 2014. Response of plants to water stress. *Frontiers of Plant Science*, *5*(86), 1–8. DOI:10.3389/fpls.2014.00086.

Pang, Y., Liu, C., Wang, D. *et al*. 2020. High-resolution genome-wide association study identifies genomic regions and candidate genes for important agronomic traits in wheat. *Molecular Plant*, *13*(9), 1311–1327. DOI:10.1016/j.molp.2020.07.008.

Parkash, V. and Singh, S. 2020. A review on potential plant-based water stress indicators for vegetable crops. *Sustainability, 12(10)*, 3945. DOI:10.3390/su12103945.

Paul, S. and Roychoudhury, A. 2018. Transgenic plants for improved salinity and drought tolerance. In Gosal, S.S. and Wani, S.H. (Eds.) *Biotechnologies of Crop Improvement*, vol. 2. New York City: Springer International Publishing AG, pp. 141–181. ISBN 978-3-319-90649-2.

Petrov, V.D. and Van Breusegem, F. 2012. Hydrogen peroxide – a central hub for information flow in plant cells. *AoB Plants*, *2012*(4), 1–13. DOI:10.1093/aobpla/pls014.

Prasad, P.V.V., Bheemanahalli, R. and Jagadish, S.V.K. 2017. Field crops and the fear of heat stress – Opportunities, challenges, and future directions. *Field Crops Research*, *200*(1), 114–121. DOI:10.1016/j.fcr.2016.09.024.

Reddy, A.R., Chaitanya, K.V. and Vivekanandan, M. 2004. Drought-induced responses of photosynthesis and antioxi-

dant metabolism in higher plants. *Journal of Plant Physiology*, *161*(11), 1189 – 1202. DOI:10.1016/j.jplph.2004.01.013.

Samarah, N.H. 2005. Effects of drought stress on growth and yield of barley. *Agronomy for Sustainable Development, 25*, (1), 145 – 149. DOI:10.1051/agro:2004064.

Saradadevi, R., Bramley, H., Palta, J.A., Edwards, E., Siddique, K.H.M. 2015. Root biomass in the upper layer of the soil profile is related to the stomatal response of wheat as the soil dries. *Functional Plant Biology*, *43*(1), 62 – 74. DOI: 10.1071/FP15216.

Saradadevi, R., Palta, J.A. and Siddique, K.H.M. 2017. ABA-mediated stomatal response in regulating water use during the development of terminal drought in wheat. *Frontiers in Plant Science*, *8*(7), 1 – 14. DOI:10.3389/fpls.2017.01251.

Savin, R., Stone, P.J., Nicolas, M.E. and Wardlaw, I.F. 1997. Grain growth and malting quality of barley. 1. Effects of heat stress and moderately high temperature. *Australian Journal of Agricultural Research*, *48*(5), 615 – 624. DOI: 10.1071/A96064.

Senapati, N., Stratonovitch, P., Paul, M.J., Semenov, M.A. 2018. Drought tolerance during reproductive development is important for increasing wheat yield potential under climate change in Europe. *Journal of Experimental Botany*, *69*(13), 1 – 12. DOI:10.1093/jxb/ery226.

Siddiqui, M.N., Mostofa, M.G., Akter, M.M., Srivastava, A.K., Sayed, M.A., Hasan, M.S. and Tran, L.S. 2017. Impact of salt-induced toxicity on growth and yield-potential of local wheat cultivars: oxidative stress and ion toxicity are among the major determinants of salt-tolerant capacity. *Chemosphere*, *187*(1), 385 – 394. DOI:10.1016/j.chemosphere.2017.08.07.

Singh, J. and Thakur, J.K. 2018. Photosynthesis and abiotic stress in plants. *Biotic and Abiotic Stress Tolerance in Plants*. Singapore: Springer, pp. 27 – 46. ISBN 978-981-10-9029-5

ŠKODÁČEK, Z. and PRÁŠIL, I.T. 2011. New possibilities for research of barley (*Hordeum vulgare* L.) drought resistance. *Úroda*, *59*(8), 24 – 29.

Souza, R.P., Machado, E.C., Silva, J.A.B., Lagôaa, A.M.M.A. and Silveira, J.A.G. 2004. Photosynthetic gas exchange, chlorophyll fluorescence and some associated metabolic changes in cowpea (*Vigna unguiculata*) during water stress and recovery. *Environmental and Experimental Botany*, *51*(1), 45 – 56. DOI:10.1016/S0098-8472(03)00059-5.

Swindell, W.R., Huebner, M., Weber, A.P. 2007. Transcriptional profiling of *Arabidopsis* heat shock proteins and transcription factors reveals extensive overlap between heat and non-heat stress response pathways. *BMC Genomics*, *22*, 8, 1 – 15. DOI:10.1186/1471-2164-8-125.

Tatar, O. and Gevrek, M.N. 2008. Influence of water stress on proline accumulation, lipid peroxidation and water content of wheat. *Asian Journal of Plant Science*, *7*, 409 – 412. DOI: 10.3923/ajps.2008.409.412

Thomas, W.T.B. 2015. Drought-resistant cereals: impact on water sustainability and nutritional quality. *Proceedings of the Nutrition Society*, *74*(3), 191 – 197. DOI:10.1017/S0029665115000026.

Tuberosa, R. and Salvi, S. 2006. Genomics-based approaches to improve drought tolerance of crops. *Trends in Plant Science*, *11*(8), 405 – 412. DOI:10.1016/j.tplants.2006.06.003.

Vílchez, J.I., García-Fontana, C., Román-Naranjo, D., González-López, J. and Manzanera, M.O. 2016. Plant drought tolerance enhancement by trehalose production of desiccation-tolerant microorganisms. *Frontiers in Microbiology*, *7*, 1577. DOI:10.3389/fmicb.2016.01577.

Vítámvás, P., Kosová, K., Musilová, J., Holková, L., Mařik, P., Smutná, P., Klíma, M. and Prášil, I.T. 2019. Relationship between dehydrin accumulation and winter survival in winter wheat and barley grown in the field. *Frontiers in Plant Science*, *10*(7), 1 – 11. DOI:10.3389/fpls.2019.00007.

Wahid, A., Perveen, M., Gelani, S. and Basra, S.M.A. 2007. Pretreatment of seed with H_2O_2 improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins. *Journal of Plant Physiology*, *164*(3), 283 – 294. DOI:10.1016/j.jplph.2006.01.005.

Wang, J., Vanga, S.K., Saxena, R., Orsat, V., RaghavaN, V. 2018. Effect of climate change on the yield of cereal crops: A review. *Climate*, *6*(2), 1 – 19. DOI:10.3390/cli6020041.

Wang, W., Vinocur, B. and Altman, A. 2003. Plant responses to drought, salinity, and extreme temperatures: towards genetic engineering for stress tolerance. *International Journal of Plant Biology*, *218*(1), 1 – 14. DOI:10.1007/s00425-003-1105-5.

Ward, J.K., Tissue, D.T., Thomas, R.B., Strain, B.R. 1999. Comparative responses of model C3 and C4 plants to drought in low and elevated CO_2. *Global Change Biology*, *5*, 857 – 867. DOI:10.1046/j.1365-2486.1999.00270.x.

Wardlaw, I.F. and Willenbrink, J. 2000. Mobilization of fructan reserves and changes in enzyme activities in wheat stems correlate with water stress during kernel filling. *New Phytologist*, *148*(3), 413 – 422. DOI:10.1046/j.1469-8137.2000.00777.x.

Zenda, T., Liu, S. and Duan, H. 2020. Adapting cereal grain crops to drought stress: 2020 and Beyond [Online First], IntechOpen, DOI:10.5772/intechopen.93845. Available from: https://www.intechopen.com/online-first/adapting-cereal-grain-crops-to-drought-stress-2020-and-beyond

Zhai, C.Z., Zhao, L., Yin, L.J., Chen, M., Wang, Q.Y., Li, L.Ch., Xu, Z.S. and MA, Y.Z. 2013. Two wheat glutathione peroxidase genes whose products are located in chloroplasts improve salt and H_2O_2 tolerances in *Arabidopsis*. *PLOS ONE*, *8*(10), 1 – 13. DOI:10.1371/journal.pone.0073989.

Zhou, H., Hussain, S.S., Hackenberg, M., Bazanova, N., Eini, O., Li, J., Gustafson, P. and Shi, B. 2018. Identification and characterisation of a previously unknown drought tolerance-associated microRNA in barley. *Plant Journal*, *95*, 138 – 149. DOI:10.1111/tpj.13938.

Zhou, Y., Lam, H.M. and Zhang, J. 2007. Inhibition of photosynthesis and energy dissipation induced by water and high light stresses in rice. *Journal of Experimental Botany*, *58*(5), 1207 – 1217. DOI:10.1093/jxb/erl291.

Received: February 2, 2021
Accepted: June 23, 2021