Abiotic Stress Tolerance in Wheat Plants

Subjects: Plant Sciences

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Wheat represents one of the most important staple food crops worldwide and its genetic improvement is fundamental to meeting the global demand of the growing population. Genetic engineering strategies such as transgenesis and genome editing have then provided the opportunity to improve environmental tolerance traits of agronomic importance in cultivated species. Many of the obtained transgenic wheat lines carried better tolerance to environmental cues. Examples of the most relevant transgenic approaches aimed at improving the tolerance of wheat to drought, salinity and extreme temperatures are reported.

wheat abiotic stresses drought salinity cold

1. Drought

Drought is probably the most important abiotic stress that limits crop productivity worldwide. It occurs when there is less-than-average precipitation over a prolonged period of time, with a consequent reduction of the atmospheric and soil moisture that leads to an imbalance between evapotranspiration flux and water absorption from the soil. Wheat is grown in different environments, but many of these environments have drought stress as one of the major challenges to its yield. Wheat is susceptible to drought particularly at the jointing stage when it grows rapidly and the impact of water stress can accumulate quickly, thus reducing yield potential in a relatively short period of time. In addition, exposure of wheat plants to drought stress conditions after flowering and until maturity reduces the period of grain filling and ripening, thus severely reducing yields [1].

Most of the candidate genes exploited to improve drought tolerance in wheat are transcription factors, which play a key role in signal transduction under drought stress by regulating the expression of downstream genes involved in plant response to water deficit. Transcription factors that have been successfully used for the improvement of wheat tolerance to drought mainly belong to the DREB/CBF (GmDREB1, AtDREB1, GhDREB, TaDREB3 and TaCBF5L) [2][3][4][5][6][7][8], ERF (TaERF3) [9], NAC (TaNAC69-1, SNAC1) [10][11], HD-ZipI (HaHB4) [12] and WRKY (TaWRKY2, AtWRKY30) [13][14] families, but they also include the ABA-stress-ripening (ASR) transcription factor (TaASR1-D), which is involved in drought tolerance through the ABA signalling [15], and the BES/BZR transcription factor (TaBZR2) [16] and the nuclear factor Y (NF–Y) subunit A (TaNF-YA7-5B) [17], which are known to be involved in the modulation of various physiological processes including response to abiotic stresses (**Table 1**). When exposed to controlled water-limited conditions these transgenic lines exhibited better growth performance and higher biomass accumulation compared to the wild-type plants. The most common responses triggered by drought in these overexpressing lines were the upregulation of ABA- and stress-responsive genes, the accumulation of compatible solutes and the activation of the antioxidant defence system, which resulted in better osmotic adjustment, higher water retention and photosynthetic efficiency, and lower ROS production and oxidative damages to plant membranes (**Table 1**). Interestingly, after exposure to drought stress, the overexpression of the *GmDREB1* gene also induced the expression of genes involved in the biosynthesis of melatonin and the concomitant increase in the melatonin levels in leaves and roots [3] (**Table 1**). In this regard, evidence exists on the role of melatonin in counteracting the deleterious effects of biotic and abiotic stresses in plants through direct scavenging of ROS and indirectly through the stimulation of plant growth regulators and the improvement of the photosynthetic and antioxidant systems [18]. Some of the wheat lines overexpressing a transcription factor were also evaluated for their tolerance to drought under field conditions. When grown under water-limited conditions in the field, the *GmDREB1* overexpressing lines exhibited better growth performances and consequently higher grain yields compared to non-transgenic plants [3] (**Table 1**). A field trial was also carried out for testing the *AtDREBA1* overexpressing lines that under greenhouse drought conditions presented a high survival rate and water use efficiency (WUE) [5]. Although under field conditions these transgenic lines did not outperform the wild-type plants, they presented more stable growth and yield performance across different environments [5] (**Table 1**). Compared to wild-type plants, wheat lines overexpressing the *HaHB4* gene grown in the open field under water-limited conditions presented better WUE and higher grain yield due to higher grain number per square meter that, in turn, was linked to higher number of spikelets per spike, tillers per plant, and fertile florets per plant [12] (**Table 1**). These findings indicate that transgenic approaches can be effective in improving wheat adaptability to marginal regions characterized by frequent drought events.

Table 1. Improvement of drought tolerance in wheat plants through transgenic approaches.

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
GmDREB1	Dehydration-responsive element-binding protein	Soybean	• Higher number of leaves and roots • Higher soluble sugar levels	[2]
			• Less membrane damage, better osmotic adjustment and photosynthetic efficiency, higher melatonin level • Upregulation of stress-responsive genes (e.g., transcription factors, antioxidant enzymes, enzymes involved in the biosynthesis of melatonin) • Higher yields in the field	[3]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
AtDREBA1	Dehydration-responsive element-binding protein	*Arabidopsis thaliana*	• Higher relative water content, higher chlorophyll, proline and soluble sugar levels	[4]
			• Higher water use efficiency and biomass • Stable yield performance under water-deficit conditions in the field	[5]
GhDREB	Dehydration-responsive element-binding protein	Cotton	• Higher survival rates • Higher soluble sugar level	[6]
TaDREB3	Dehydration-responsive element-binding protein	Bread wheat	• Higher survival rates and higher yields	[7]
TaCBF5L	C-repeat binding factor	Bread wheat	• Higher plant biomass and grain weight	[8]
TaERF3	Ethylene response factor	Bread wheat	• Higher survival rates and lower water loss • Upregulation of ABA- and stress-responsive genes (e.g., peroxidase, late embryogenesis abundant protein, ABA-responsive protein, glutathione-*S*-transferase)	[9]
TaNAC69-1	Protein belonging to the NAM/ATAF1-2/CUC2 family	Bread wheat	• Higher root and shoot biomass and longer roots • Enhanced expression of stress-responsive genes	[10]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
SNAC1	Protein belonging to the NAM/ATAF1-2/ CUC2 family	Rice	• Higher water retention and chlorophyll content • Enhanced expression of genes involved in ABA signalling (e.g., sucrose phosphate synthase, 1-phosphatidylinositol-3-phosphate 5-kinase, type 2C protein phosphatases, and regulatory components of ABA receptor)	[11]
HaHB4	Homeodomain-leucine zipper I protein	Sunflower	• Higher water use efficiency • Higher number of spikelets per spike, tillers per plant, and fertile florets per plant and higher yields	[12]
TaWRKY2	WRKY domain protein	Bread wheat	• Higher soluble sugars, proline and chlorophyll levels and lower hydrogen peroxide levels at seedling stage • Longer spike length, more kernels per spike, greater aboveground biomass, higher yields	[13]
AtWRKY30	WRKY domain protein	*Arabidopsis thaliana*	• Higher shoot and root length, and biomass production • Higher chlorophyll, proline and soluble sugar levels and antioxidant enzymes activities • Higher photosynthetic performance and higher relative water content	[14]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
			• Lower malondialdehyde, hydrogen peroxide levels and electrolyte leakage • Upregulation of stress-responsive genes (e.g., antioxidant enzymes, transcription factors and aquaporins)	
TaASR1-D	Abscisic acid stress-ripening protein	Bread wheat	• Higher survival rates and greater water retention ability	[15]
TaBZR2	BRI1-EMS suppressor /brassinazole-resistant family	Bread wheat	• Higher survival rates, delayed leaf rolling, and proline level • Lower malondialdehyde and electrolyte leakage • Upregulation of abiotic stress-responsive genes	[16]
TaNF-YA7-5B	Nuclear factor Y transcription factors	Bread wheat	• Higher shoot and root length, and biomass production • Fasta stomata closing rates and reduced water losing rates • Higher proline and soluble sugar levels and antioxidant enzyme activities • Lower malondialdehyde and ROS levels • Higher photosynthetic performance • Upregulation of stress-responsive genes (e.g., Δ^1-pyrroline-5-carboxylate	[17]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
			synthase, superoxide dismutase and catalase)	
Osmolytes				
P5CS	Δ^1-pyrroline-5-carboxylate synthase	*Vigna aconitifolia*	• Higher proline level, lower malondialdehyde level and higher membrane stability	[19] [20] [21]
AtOAT	Ornithine aminotransferase	*Arabidopsis thaliana*	• Higher proline level and survival rates • Upregulation of genes involved in proline biosynthesis via glutamate and ornithine pathways and downregulation of genes involved in proline catabolism	[22]
mtlD	Mannitol-1-phosphate dehydrogenase	*Escherichia coli*	• Higher mannitol level, fresh weight, dry weight, plant height and flag leaf length	[23]
betA	Choline dehydrogenase	*Escherichia coli*	• Higher glycine betaine, proline and soluble sugar levels • Higher germination percentage and biomass, and better-developed roots • Higher relative water content, and better photosynthesis • Higher activity of antioxidant enzymes, lower malondialdehyde level and electrolyte leakage	[24]
BADH	Betaine aldehyde dehydrogenase	*Atriplex hortensis*	• Higher glycine betaine, proline, soluble protein, soluble sugar and free amino	[25]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
			acid levels • Higher relative water content, more negative osmotic potential and higher photosynthetic efficiency • Higher activity of antioxidant enzymes, lower ROS and malondialdehyde levels, and lower electrolyte leakage	
LEA proteins				
HVA1	Group 3 LEA protein	Barley	• Higher water use efficiency, root fresh and dry weights, shoot dry weight and total dry biomass	[26]
			• Higher germination rate and root length • Higher relative water content, and more negative water potential • Higher stomatal conductance and photosynthetic activity • Lower electrolyte leakage and higher membrane stability	[27]
			• Greener leaf and more robust root growth • Upregulation of drought-responsive genes (e.g., DREB and NAC transcription factors, dehydrins, ferritin, glutathione-*S*-transferase)	[28]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
			• Higher germination percentage, seedling growth, biomass accumulation and nitrate reductase activity at seedling stage • Higher photosynthetic activity and yield at post-anthesis	[29]
			• Higher water use efficiency, relative water content and stable yields in the field	[30]
ROS detoxification				
TaNRX	Thioredoxin	Bread wheat	• Higher survival rates, higher chlorophyll, proline and soluble sugar levels, higher catalase, superoxide dismutase and peroxidase activities • Lower malondialdehyde, hydrogen peroxide and superoxide anion levels • Upregulation of genes encoding transcription factors and other stress-responsive genes	[31]
MsALR	Aldose reductase	*Medicago sativa*	• Higher water use efficiency and biomass production	[32]
Other genes				
PEPC	Phosphoenolpyruvate carboxylase	Maize	• Higher proline, soluble sugar and soluble protein levels	[33]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
[21][22][23][24][25][39]	[22] [25]	[23]	• Higher water use efficiency and photosynthetic rate, higher root volume and activity, biomass per plant, spike numbers per plant, grain numbers per spike and thousand grain weight, higher levels of proteins related to photosynthesis, energy metabolism, amino acid synthesis, protein synthesis and assembly, and cytoskeleton	
TaPEPKR2	Phosphoenolpyruvate carboxylase kinase-related kinase	Bread wheat	• Higher total root length [19][20][21]	[34]
SeCspA, *SeCspB*	Cold shock proteins	[23] *Escherichia coli*	• Higher survival rates and proline level, and lower malondialdehyde level • Upregulation of stress-responsive genes • Higher yield in the field (only for *SeCspA*) [24][25]	[35]
IPT	[40] Isopentenyl transferase 2	*Agrobacterium tumefaciens*	• Delayed senescence, higher yield due to a higher number of grains per spike and a higher number of spikes in the field [33]	[36] 2
OTS1	cysteine protease (OVERLY TOLERANT TO SALT-1)	*Arabidopsis thaliana*	• Higher growth and delayed senescence • Higher relative moisture content, chlorophyll content and photosynthesis rate • [34] Lower SUMOylation of total proteins	[37]

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In addition to the main classes of candidate genes, other genes known to be involved in the response to abiotic stresses of plants and other organisms have been exploited to enhance drought tolerance in wheat. Successful examples are the bacterial *SeCspA* and *SeCspB* genes [35], which encode cold shock proteins that protect bacteria

Gene Transcription factors	Gene Product	[41] Plant Source	Improved Traits	Ref.
			[36]	
TaPYL4	ABA receptor	[38] Bread wheat	Lower stomatal opening and water loss Higher photosynthetic efficiency Higher grain yields	[38]

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2. Salinity

Worldwide, the area affected by salt stress amounts to 20% of the arable area but it is gradually increasing due to climate change and anthropogenic activities [42]. Soil salinity negatively affects wheat growth from germination to harvesting; it reduces seed germination and seedling vigour by negatively affecting root length and plant height and alters many physiological and biochemical processes; this leads to a significant decline in grain yield and quality [43]. The deleterious effects of salt are due to (i) a decreased rate of water uptake into plants due to the low water potential of soil and (ii) increased uptake of toxic ions, the accumulation of which in the plant cell causes nutritional imbalance [44].

As already highlighted, drought and salt stress have similar effects on plants; so, several genes successfully exploited to improve wheat tolerance to water deficit have also been shown to be useful in inducing salt stress tolerance in this crop. These ‘multi-protecting’ genes mainly include those encoding transcription factors, as well as enzymes involved in the biosynthesis and accumulation of osmolytes. So, wheat lines overexpressing the *GmDREB* [2], *AtDREB1A* [4], *GhDREB* [6], *TaERF3* [9], *SNAC1* [11] and *TaASR1-D* [15] genes were found to be more tolerant not only to drought but also to salinity (**Table 2**). Improved tolerance to salt stress was also achieved by overexpressing the wheat *TabZIP15* gene [45], encoding a bZIP transcription factor, as well as the *Eutrema salsugineum EsMYB90* gene [46] and the wheat *TaMYB86B* gene [47] encoding MYB transcription factors (**Table 2**). When exposed to high salt levels, the physiological, biochemical and molecular mechanisms observed in all these transgenic lines were similar to those observed under drought stress conditions, that is the upregulation of ABA- and abiotic stress-responsive genes, the accumulation of osmolytes and the activation of the antioxidant enzyme system, which resulted in lower ROS accumulation and reduced oxidative damage to membranes, and better growth performance (**Table 2**). Interestingly, the analyses of the yield parameters revealed that the grain yield of both *TabZIP15* and *TaASR1-D* overexpressing lines was increased under salt stress conditions compared to wild-type plants, thus suggesting that these genes can be useful to breed new wheat cultivars with tolerance to high salt conditions (**Table 2**).

As regards the genes involved in the biosynthesis of osmolytes, increased tolerance to salinity was observed in wheat lines overexpressing the *AtOAT* [22], *mtlD* [23][48], *betA* [49] and *BADH* [50][51][52] genes (**Table 2**). As already observed under drought stress conditions, the overexpression of these genes under salinity contributed not only to a better osmotic adjustment but also to a better control of ROS production, which reduced damages to membranes and macromolecules and resulted in higher photosynthetic activity and better growth (**Table 2**). Moreover, the analysis carried out on *mtlD*, *betA* and *BADH* overexpressing lines revealed that the overproduction of osmolytes also contributed to protecting leaves from ion toxicity; indeed, transgenic lines accumulated Na^+ and Cl^- in their sheaths and maintained higher levels of K^+ in their leaves, thus reducing the leaf Na^+/K^+ ratio compared to non-transgenic plants (**Table 2**). In terms of grain yields and grain quality, the field performance of the *mtlD* and *betA* overexpressing lines in saline land areas was much better than the wild-type plants (**Table 2**), thus showing the promising potential of these genes in salt-tolerant wheat breeding.

A similar mechanism of tolerance to salinity was observed in wheat lines overexpressing the *HVA1* gene from barley. In addition to better seed germination, root and shoot development, lower electrolyte leakage and higher membrane stability, these lines presented lower Na^+ levels in the shoot compared to non-transgenic plants [27] (**Table 2**), a phenomenon that could be linked to the ability of LEA 3 proteins to sequestrate ions under stress conditions [53].

Among the genes involved in ROS detoxification, the overexpression of the wheat peroxidase (*TaPRX-2A*) gene was found to be effective in improving wheat tolerance to salt stress [54] (**Table 2**). As observed under drought stress in wheat lines overexpressing the *TaNRX* gene (see **Table 1**), the overexpression of the *TaPRX-2A* gene exerted its positive action against salinity both directly and indirectly through the activation of other antioxidant enzymes. Indeed, the wheat lines overexpressing the *TaPRX-2A* gene showed not only higher peroxidase activity, but also higher catalase and superoxide dismutase activities, as a consequence of an upregulation of their encoding genes; this amplified the antioxidant reaction and effectively lowered the salt-induced cell oxidation, as demonstrated by the stronger reduction of ROS and MDA levels compared to non-transgenic plants (**Table 2**). Since TaPRX-2A was found to be located in the nucleus, it is feasible that its role under salt stress is the inhibition of ROS-mediated damage to genomic DNA, whereas the other antioxidant enzymes are responsible for ROS scavenging in other cell compartments.

A class of candidate genes typically involved in the plant response to salt stress is represented by aquaporins and ion transporters, which regulate water, and Na^+ and K^+ transport. Wheat lines overexpressing genes encoding aquaporins of the PIP type, such as the *SbPIP1* gene from *Salicornia bigelovii* [55], a euhalophyte that requires high Na^+ concentration for optimal growth, and the durum wheat *TdPIP2;1* gene [56], performed much better in physiological and biochemical attributes compared to wild-type plants, showing higher osmolyte levels and antioxidant activity, as well as lower Na^+/K^+ ratio, which resulted in better osmotic adjustment, lower oxidative damage and better growth performance (**Table 2**). Interestingly, in a long-term experiment, the *TdPIP2;1* overexpressing lines reached maturity and produced filled grains (**Table 2**), thus suggesting they could be potentially cultivated in saline soils without major penalties for grain yield. Although the molecular basis underlying salinity tolerance in the wheat lines overexpressing the *PIP* genes was not investigated, it is feasible that the complex response observed in the *PIP* overexpressing lines is due not only to the higher PIP levels in the plasma membrane but also to PIP-induced upregulation of other stress-responsive genes, as already observed in other plant species overexpressing foreign aquaporin genes [57]. Higher salinity tolerance was also observed in the wheat lines overexpressing the *Arabidopsis AtNHX1* gene [58], which encodes the vacuolar Na^+/H^+ antiporter, and the barley vacuolar H$^+$-pyrophosphatase (*HVP1*) gene [59], which encodes the proton pump that generates the proton gradient needed to promote Na$^+$/H$^+$ antiport. In both cases, the overexpressing lines presented higher germination rate and biomass accumulation compared to non-transgenic plants; moreover, when grown under saline field conditions, they also presented higher yields (**Table 2**). This is expected since, in addition to leaf Na$^+$ exclusion, the mechanism of tissue tolerance, based on Na$^+$ compartmentalization into the vacuole, represents a major mechanism of salinity tolerance in wheat [60]. Under salinity, lower Na$^+$ levels were also detected in wheat plants overexpressing the bacterial *SeCspA* and *SeCspB* genes [35], and the wheat bile acid/sodium symporter 2 (*TaBASS2*) gene, responsible for the uptake into chloroplast of pyruvate, a precursor of ABA and other metabolites involved in plant response to stress [61] (**Table 2**). Lower Na$^+$ and higher K$^+$ levels were observed in wheat lines overexpressing the *TaPUB1* gene encoding a U-box E3 ubiquitin ligase, a component of the ubiquitin–proteasome pathway that regulates the activity and stability of many cellular proteins and is involved in diverse physiological processes including responses to abiotic stress [62]. When exposed to salt stress, these transgenic lines also exhibited higher proline levels and higher activities of antioxidant enzymes that contributed to a better control of ROS production compared to wild-type plants (**Table 2**). Transcriptional analysis revealed that these physiological responses are a consequence of the TaBUB1-induced upregulation of genes encoding ion transporters and enzymes involved in proline biosynthesis and ROS scavenging (**Table 2**).

Table 2. Improvement of salinity tolerance in wheat plants through transgenic approaches.

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
GmDREB1	Dehydration-responsive element-binding protein	Soybean	- More extended leaves and plentiful roots	[2]
AtDREBA1	Dehydration-responsive element-binding protein	*Arabidopsis thaliana*	- Higher relative water content, chlorophyll, proline and soluble sugar levels	[4]
GhDREB	Dehydration-responsive element-binding protein	Cotton	- Higher survival rates and chlorophyll content	[6]
TaERF3	Ethylene response factor	Bread wheat	- Higher germination and survival rates - Higher chlorophyll level, lower hydrogen peroxide level and lower stomatal conductance	[9]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
			• Upregulation of ABA- and stress-sensitive genes (e.g., peroxisase, late embryogenensis abundant protein, ABA-responsive protein, glutathione-*S*-transferase)	
SNAC1	Protein belonging to the NAM/ATAF1-2/CUC2 family	Rice	• Higher survival rates and grain number • Upregulation of the expression of ABA- and stress-sensitive genes and genes encoding regulatory components of ABA receptor	[11]
TaASR1-D	Abscisic acid stress-ripening protein	Bread wheat	• Higher plant height, dry biomass, tiller number, spikelet number per spike, grain yield per plant, grain weight and grain width • Lower superoxide anion, hydrogen peroxide and malondialdehyde levels	[15]
TabZIP15	Basic leucine zipper proteins	Bread wheat	• Higher plant height, longer root length, higher aboveground and root fresh weight, longer spike length, higher number of grains per spike • Lower malondialdehyde and hydrogen peroxide levels • Upregulation of genes involved in metabolic processes and response to abiotic stresses	[45]
EsMYB90	v-myb avian myeloblastosis viral oncogene homolog family	*Eutrema salsugineum*	• Higher root length and fresh weight, higher peroxidase and glutathione	[46]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
TaMYB86B	v-myb avian myeloblastosis viral oncogene homolog family	Bread wheat	• Higher biomass and K$^+$ level • Lower Na$^+$, ROS and malondialdehyde levels, upregulation of stress-related genes	[47]
Osmolytes				
AtOAT	Ornithine aminotransferase	*Arabidopsis thaliana*	• Higher proline and chlorophyll levels, and higher peroxidase and catalase activities • Faster growth, higher survival rates, longer and more secondary roots and longer shoots • Upregulation of genes involved in proline biosynthesis via glutamate and ornithine pathways and downregulation of genes involved in proline catabolism	[22]
mtlD	Mannitol-1-phosphate dehydrogenase	*Escherichia coli*	• Higher mannitol levels • Higher shoot fresh weight, dry weight, plant height and flag leaf length	[23]
			• Higher proline, mannitol, soluble sugar, chlorophyll and K$^+$ levels, and higher activities of enzymatic and non-enzymatic antioxidants • Higher number of leaves and leaf area per plant, root system size and plant dry weight	[48]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
			Higher number of spikes and grain weight per plant, and thousand grain weight Higher grain content of starch, protein and soluble sugars	
betA	Choline dehydrogenase	*Escherichia coli*	Higher glycine betaine, proline and soluble sugar levels Higher relative water content and more negative osmotic potential Lower Na^+/K^+ ratio, malondialdehyde level and electrolyte leakage Higher germination rates, more tillers and higher grain yields in the field	[49]
BADH	Betaine aldehyde dehydrogenase	*Atriplex hortensis*	Higher glycine betaine, proline, and soluble protein and sugar levels, and higher activity of antioxidant enzymes Better osmotic adjustment, lower Na^+ and higher K^+ levels in the leaves Lower ROS and malondialdehyde levels, and lower electrolyte leakage	[50]
			Higher glycine betaine, chlorophyll and carotenoid levels Modification of the lipid composition of thylakoid membranes and higher photosynthetic activity	[51]

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
HvBADH1	Betaine aldehyde dehydrogenase	Barley	- Higher glycine betaine and K^+ levels - Higher survival rates	[52]
LEA proteins				
HVA1	Group 3 LEA protein	Barley	- Higher germination rate and root length - Lower electrolyte leakage and higher membrane stability - Lower Na^+/K^+ ratio in the shoot	[27]
ROS detoxification				
TaPRX-2A	Peroxidase	Bread wheat	- Higher survival rates and shoot length - Higher relative water content - Higher proline, soluble sugar and soluble protein levels - Higher peroxidase, catalase and superoxide dismutase activities - Lower malondialdehyde, superoxide anion and hydrogen peroxide levels - Upregulation of ABA- and stress-responsive genes (e.g., ROS scavenging enzymes, thumatin-like protein, glutathione *S*-transferase)	[54]
Aquaporins and ion transporters				

Gene Transcription factors	Gene Product	Plant Source	Improved Traits	Ref.
SbPIP1	Plasma membrane intrinsic proteins	*Salicornia bigelovii*	• Higher proline and soluble sugar levels and lower malondialdehyde level	[55]
TdPIP2;1	Plasma membrane intrinsic proteins	Durum wheat	• Higher catalase and superoxide dismutase activities, and lower malondialdehyde and hydrogen peroxide levels • Lower Na^+ level and higher K^+ level in the shoots • Higher germination rate, higher biomass and filled grains	[56]
AtNHX1	Vacuolar Na^+/H^+ antiporter	*Arabidopsis thaliana*	• Lower Na^+ and higher K^+ levels in the leaves • Higher germination rates, biomass production, and heavier and larger grains in the field	[58]
HVP1	Vacuolar pyrophosphatase	Barley	• Higher photosynthesis rate, stomatal conductance, transpiration rate and water use efficiency • Higher germination rate, plant height, spike length, number of spikelets per spike, 1000 grain weight, grain yield and harvest index in the field	[59]
Other genes				
SeCspA, *SeCspB*	Cold shock proteins	*Escherichia coli*	• Higher fresh weight and lower Na^+ content	[35]

resents a peratures ctivity [63]. Wheat can be subjected to heat stress conditions throughout its growth cycle; however, the greatest damages occur when high temperatures coincide with the reproductive and grain filling stages of this crop. The persistence of high temperatures during these stages reduces both grain yield and quality. It has been estimated that for each 1

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors	[64]		[65]	
TaBASS2 [14]	Pyruvate transporter	Bread wheat	- Lower Na$^+$ level and ROS scavenging	[61]
TaPUB1 [67]	U-box E3 ubiquitin ligase [68]	Bread wheat	- Longer shoot and root - Higher chlorophyll, proline and soluble sugar levels - Higher photosynthetic rate, transpiration rate and stomatal conductance - Higher catalase, superoxide dismutase and peroxidase activities - Lower malondialdehyde, superoxide anion and hydrogen peroxide levels [69][70] - Lower Na$^+$ and higher K$^+$ levels in the root [71] - Upregulation of stress-responsive genes (e.g., ion transporters, antioxidant enzymes and enzymes involved in proline biosynthesis) [72][73]	[62]

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shown to be effective in increasing tolerance to high temperatures. These include the *AtOAT* gene [22] and the *BADH* gene from *Atriplex hortensis* [25] involved in the accumulation of osmolytes, the *HVA1* gene from barley [28], and the *ZmPEPC* [74] and the Ta*PEPKR2* [34] genes involved in the CO_2 fixation in C4 and Crassulacean plants. However, in addition to responses similar to other abiotic stresses, specific responses to heat stress were also observed in these transgenic lines. Indeed, as already observed under water and salt stress, heat-stressed wheat lines overexpressing the *AtOAT* gene exhibited the activation of the glutamate pathway for proline biosynthesis, but unlike the other two stress conditions, heat stress did not induce proline biosynthesis via the ornithine pathway, and this was probably the reason why tolerance to high temperatures was only partial [22] (**Table 3**). Furthermore, the accumulation of glycine betaine due to the overexpression of the BADH gene from *Atriplex hortensis* counteracted the heat stress by improving the photosynthetic capacity, as already observed under drought stress; but whereas the improvement of photosynthesis observed under drought stress was due to an osmotic adjustment, under heat stress it was mainly due to the activation of the antioxidant system, which reduced the accumulation of ROS and the peroxidation of membrane lipids [25] (**Table 3**). Similarly, in the wheat lines overexpressing the *HVA1* gene, the response triggered by exposure to heat stress was mainly directed towards the control of ROS production (**Table 3**) rather than to the increase in water retention, as observed when these transgenic lines were exposed to drought

(see **Table 1**). A possible explanation emerges from the transcriptomic analysis. Indeed, while drought stress induced the expression of *DREB* and *NAC* genes (see **Table 1**), exposure to a high temperature determined the upregulation of *HPS* and *HSF* genes (**Table 3**). As observed under drought stress conditions, wheat lines overexpressing the *ZmPEPC* gene, when exposed to high temperature, showed a higher photosynthetic rate and better growth performance compared to non-transgenic plants (**Table 3**). Consistently, transcriptomic analysis on heat-stressed lines revealed the upregulation of photosynthesis-related genes (**Table 3**), which is in line with the higher levels of photosynthesis-related proteins observed in the same lines exposed to drought stress (see **Table 1**). Moreover, under heat stress, these transgenic lines also presented the higher activity of antioxidant enzymes, which resulted in lower ROS levels and reduced oxidative damage (**Table 3**).

Table 3. Improvement of heat tolerance in wheat plants through transgenic approaches.

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
AtWRKY30	WRKY domain protein	*Arabidopsis thaliana*	• Higher shoot and root length, and biomass production • Higher chlorophyll, proline and soluble sugar levels, and antioxidant enzymes activities • Higher photosynthetic performance and higher relative water content • Lower malondialdehyde and hydrogen peroxide levels, and electrolyte leakage • Upregulation of stress-responsive genes (e.g., antioxidant enzyme, transcription factors and aquaporins)	[14]
TaHsfC2a-B	Heat shock factor	Bread wheat	• Higher survival rates, shoot and root length and dry biomass • Higher chlorophyll content and lower electrolyte leakage • Upregulation of heat shock protein genes and other ABA- and stress-responsive	[69]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
			genes (e.g., galactinol synthase, heat-stress-associated 32-KD protein, α-amylase, filamentation temperature sensitive family metalloprotease and calcium-binding EF-hand family protein)	
TaHsfA6f	Heat shock factor	Bread wheat	• Longer shoot and higher number of roots • Upregulation of heat shock protein genes and other stress-responsive genes (e.g., Rubisco activase large isoform, Golgi anti-apoptotic protein and glutathione-S-transferase)	[70]
Chaperones				
Zmeftu1	Elongation Factor thermo-unstable	Maize	• Lower thermal aggregation of leaf proteins and heat injury to thylakoid membranes • Higher rate of CO_2 fixation	[72]
			• Higher number of grains per plant, total grain mass per plant, and single grain mass	[73]
Osmolytes				
AtOAT	Ornithine aminotransferase	*Arabidopsis thaliana*	• Higher proline level • Upregulation of genes involved in proline biosynthesis via glutamate pathway and downregulation of genes involved in proline catabolism	[22]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
BADH	Betaine aldehyde dehydrogenase	*Atriplex hortensis*	• Higher glycine betaine level • Higher catalase, superoxide dismutase and peroxidase activities • Lower hydrogen peroxide, superoxide anion and malondialdehyde levels	[25]
LEA proteins				
HVA1	Group 3 Late Embryogenesis Abundant protein	Barley	• Lower superoxide anion and hydrogen peroxide levels • Larger spikes and grain size, and higher grain weight • Upregulation of stress-responsive genes (e.g., *HsfA6* transcription factor, HSPs, glutathione-S-transferase, ferrodoxin, ABA-induced plasma membrane protein PM19, caleosin, cytochrome P450 and haem peroxidase)	[28]
ROS detoxification				
TaFER-5B	Ferritin	Bread wheat	• Lower ROS levels and membrane damages • Higher photosynthetic activity	[75]
Other genes				
ZmPEPC	Phosphoenolpyruvate carboxylase	Maize	• Higher chlorophyll levels, photosynthetic rate, superoxide dismutase, catalase and peroxidase activities	[74]

Gene	Gene Product	Plant Source	Improved Traits	Ref.
Transcription factors				
[75]	[76]		• Lower superoxide anion, hydrogen peroxide and malondialdehyde levels • Upregulation of photosynthesis-related genes (e.g., phosphoenolpyruvate carboxykinase, fructose bisphosphatase and triose phosphate translocator)	
TaPEPKR2	[77] Phosphoenolpyruvate carboxylase kinase-related kinase	Bread wheat	• Lower wilting [78] • Lower electrolyte leakage	[34]
SSI	Soluble starch synthase [79]I	Rice	• Longer grain filling period • Higher thousand grain weight	[76]

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4. Low Temperatures

Wheat plants are most sensitive to low temperatures during the reproductive stage when a sudden overnight drop of temperatures only a few degrees below 0° C can damage the sensitive reproductive tissues, thus resulting in spike (partial) sterility and significant yield losses [80]. In its vegetative stages, wheat can tolerate freezing temperatures up to −20 °C through cold acclimation after being exposed for a prolonged period to low temperatures between 0 and 5 °C [81]. The acquisition of freezing tolerance is carried out through many transcriptional and biochemical changes, including the activation of cold-regulated genes, the modification of membrane lipid composition, the accumulation of osmolytes and other protective and antifreeze proteins [81].

Like other abiotic stresses, tolerance to low temperatures has been achieved by overexpressing genes encoding transcription factors and enzymes involved in the biosynthesis of osmolytes. Indeed, improved tolerance to freezing was observed in transgenic wheat lines overexpressing the cotton *GhDREB* gene [6] and the *BADH* gene from *Atriplex hortensis* [82]. When exposed to freezing temperatures, the *GhDREB* transgenic lines grew normally, whereas the growth of wild-type plants was retarded, with survival rates significantly higher in the former compared to the latter. As already observed for the other stresses, transgenic lines overexpressing the *BADH* gene and exposed to cold stress exhibited higher levels of glycine betaine, proline and soluble sugars [82], which may all function as cryoprotectants by helping to protect membrane proteins and enzymes from cold-induced damages. Consistently, the cold-stressed transgenic lines maintained better membrane integrity and functionality compared to wild-type plants, as demonstrated by the lower electrolyte leakage and the higher activity of the plasma membrane H^+-ATPase. Under cold stress, these transgenic lines also presented lower ROS production and membrane lipid peroxidation compared to non-transgenic plants [82]. This may be ascribable both to the ability of osmolytes to act as ROS scavengers and to protect the structure and the activity of the antioxidant enzymes, as demonstrated by the higher catalase and peroxidase activities detected under cold stress in the *BADH* overexpressing lines compared to wild-type plants.

The protection of plant membranes from cold-induced damage has been achieved also by overexpressing the *BLT101* gene from barley [83]. This gene encodes a lipid transfer protein (LTP) able to modulate the local lipid composition and fluidity of plant membranes [84] and is upregulated in barley plants exposed to cold stress [85]. Consistently, wheat plants overexpressing the barley *BLT101* gene exhibited reduced leakage of intracellular substances and enhanced freezing tolerance compared to the wild-type plants; in addition, the transgenic lines that underwent cold acclimation maintained higher water content compared to wild-type plants.

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