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Table

Increasing drought tolerance of wheat via genetic transformation

Gene and its origin	Product	Function	Improved traits in transgenic plants	Reference
Functional genes				
Genes, encoding osmoprotectors				
VaP5CS (*Vigna aconitifolia)*	delta-1-pyrroline-5-carboxylate-synthetase (P5CS)	Proline synthesis via glutamate. Protection from oxidative stress, support for cell turgor and stability of membranes and proteins, decrease in damage to cell structures and decrease in ROI level.	Higher proline level, lower level of malondialdehyde, and higher stability of cellular membrane.	Vendruscolo et al., 2007; Pavei et al., 2016; De Lima et al., 2019
AtOAT *(Arabidopsis thaliana)*	ornithine-δ-aminotrans-ferase (OAF)	Proline synthesis via ornithine. Protection from oxidative stress, support for cell turgor and stability of membranes and proteins, decrease in damage to cell structures and decrease in ROI level.	Proline accumulation and higher survival rate, higher activity of peroxidase.	Anwar et al., 2021
MtOAT *(Medicago truncatula)*			Larger weight and length of the roots, better photosynthetic activity, increased productivity.	Dubrovna et al., 2021; Mykhalska et al., 2021
AtProDH *(Arabidopsis thaliana)*	proline dehydrogenase (ProDH)	Proline catabolism. Support for the energy balance of cells, regulation of redox homeostasis, ROI detoxication.	Proline accumulation, increase in the activity of the antioxidant system, better photosynthetic activity.	Dubrovna et al., 2020, 2022a,b
BADH *(Atriplex hortensis*)	betaine aldehyde	Synthesis of glycine betaine. Catalizes the transformation of betaine aldehyde into glycine betaine. Osmotic and antioxidant	Higher content of glycine betaine, proline, and level of soluble sugar. Decreased photoinhibition of	Wang et al., 2010a,b

	dehydrogenase (BADH)	protection, stabilization of membranes and proteins, support for water balance and photosynthetic activity.	photosystem II, improved system of antioxidant protection. Higher relative content of water, lower outflow of electrolyte.	
betA (*Escherichia coli*)	choline dehydrogenase (betA)	Synthesis of glycine betaine. Catalyzes the transformation of choline into betaine aldehyde. Osmotic and antioxidant protection, stabilization of membranes and proteins, support for water balance and photosynthetic activity.	Higher content of glycine betaine, proline, and level of soluble sugar. Better germination and biomass of plants, better developed roots. Higher relative content of water and better photosynthesis. Higher antioxidant activity of enzymes, lower content of malondialdehyde.	He et al., 2011
mtlD *(Escherichia coli*)	Manitol-1-phosphate dehydrogenase (mtlD)	Manitol synthesis. Catalyzes the reverse transformation of Fru-6-phosphate into manitol-1-phosphate. Osmotic and antioxidant protection, stabilization of membranes and proteins, support for photosynthetic activity.	Mannitol accumulation. Larger biomass, height of plants, and length of the flag leaf.	Abebe et al., 2003
TPS1, TPS2 *(Saccharomyces cerevisiae*)	Trehalose-6-phosphate synthase (TPS1), trehalose-6-phosphate phosphatase (TPS2)	Trehalose synthesis. TPS1 catalyzes the formaiton of trehalose-6-phosphate (T6P), TPS2 transforms T6P into trehalose. Protection from osmotic and oxidative stress, stabilization of proteins and membranes, regulation of metabolism processes.	Trehalose accumulation. Increase in the length of the spikelet, height of plants, number and weight of grain from the main spikelet.	Kvasko et al., 2020
Genes, encoding cold-shock proteins				
SeCspA, SeCspB *(Escherichia coli*)	synthetic bacterial proteins (cold-	Enhance adaptation to water deficit. Support for cell turgor, stabilization of membranes and cell metabolism. Improved water balance.	Lower velocity of water loss, lower content of malondialdehyde, higher content of chlorophyll, proline, higher	Yu et al., 2017

	shock proteins, Csp)		grain yield in the field (only for SeCspA).	
Genes, encoding proteins of late embryogenesis				
HVA1 (*Hordeum vulgare*)	protein (HORDEUM VULGARE ALEURONE1) (HVA1)	Molecular chaperone. Support for structures of proteins and membranes, turgor pressure, higher efficiency of water usage and photosynthetic activity, decrease in ROI level.	Higher efficiency of water usage, larger weight of roots, and total biomass.	Sivamani et al., 2000
			Higher efficiency of water usage, larger height of plants, greater biomass accumulation, grain yield.	Bahieldin et al., 2005
			Higher relative content of water. Higher germination of seeds and length of the roots. Higher airway permeability and photosynthetic activity. Lower outflow of electrolytes and better stability of membranes.	Habib et al., 2022
			Higher percentage of seed germination, better growth of shoots, biomass accumulation, activity of nitrate reductase. Higher photosynthetic activity and yield.	Chauhan, Khurana, 2011
			Greener leaves, better growth, and developed root system. Improved regulation of TF DREB and NAC, ferritin, glutathione-S-transferase.	Samtani et al., 2022
Genes, encoding transport proteins and ions				
TdPIP2;1 (*Triticum durum*)	protein of inner plasma membrane (PIP2;1)	Aquaporin. Regulation of water transportation and closing of airways, control of cell homeostasis, higher stability of cell membranes.	Higher germination indices, larger biomass. Activation of antioxidant enzymes, lower content of malondialdehyde, and hydrogen peroxide.	Ayadi et al., 2019

TaNHX2 *(Triticum aestivum)*	protein of vacuolar K^+/H^+ antiporter	Transporter of K^+. Takes part in homeostasis of K^+, turgor generation. Regulates the airway aperture, mediating active release of potassium from vacuoles.	Higher survival rate. Higher relative content of water. Increase in the size of grain and 1,000 grain weight. Increase in the yield.	Li et al., 2024
Genes, encoding proteins and enzymes — ROI absorbents				
TaNRX1 *(Triticum aestivum)*	protein nucleoredoxin (NRX)	Regulates the activity of catalase, enhances its detoxification ability, and protects antioxidant enzymes from ROI-induced oxidative stress.	Larger weight and length of roots, higher survival rate, content of chlorophyll, proline, sugar, photosynthesis productivity and activity of antioxidant enzymes.	Zhang et al., 2021
MsALR *(Medicago sativa)*	aldose reductase (ALR)	Metabolization of cytotoxic substances, obtained by peroxide oxidation of lipids, participation in the support for water balance.	Higher efficiency of water usage and greater biomass accumulation.	Fehér-Juhász et al., 2014
TaPRX-2A *(Triticum aestivum)*	peroxidase (PRX)	Oxidation of phenol substances to decrease the level of H_2O_2. Strengthening of cell walls, regulation of growth and development.	Higher activity of antioxidants and decrease in ROI content, increase in expression of genes, related to stress and ABA. Higher survival rate, longer shoots, and higher relative content of water.	Su et al., 2023
TaFER-5B *(Triticum aestivum)*	protein ferritin (FER)	Accumulation and preservation of iron, transformation of toxic Fe^{2+} into non-toxic chelate complex. Neutralization of free radicals, prevention of the formation of hydroxyl radicals. Support for the stability of cell structures and membranes, decrease in ROI amount.	Accumulation of iron in leaves, longer roots, lower damage to the membrane, better photosynthetic activity.	Zang et al., 2017
Genes, encoding the cellular wall proteins				

TaEXPA2 *(Triticum aestivum)*	protein α-expansin (EXP)	Extension of the cellular wall. Stabilization of cellular structures, support for water balance.	Higher survival rate, photosynthesis velocity, and the ability to keep water. Higher activity of antioxidant enzymes. Extensive formation of side roots.	Yang et al., 2020a
Genes, encoding the enzymes, related to carbon metabolism				
PEPC *(Zea mays)*	phosphoenolpyruvate carboxylase (PEPC)	Control of primary fixation of CO_2 in plants with C4 photosynthesis Activation of metabolic pathways, preservation of energy balance. Enhanced efficiency of water usage and photosynthetic activity.	Higher content of proline, soluble sugar, and protein. Higher efficiency of water usage and photosynthesis velocity, biomass, number and weight of grain. Higher level of proteins, related to photosynthesis and synthesis of aminoacids.	Qin et al., 2016
PEPC, PPDK *(Zea mays)*	phosphoenolpyruvate carboxylase (PEPC), pyruvate orthophosphate dikinase (PPDK)	PPDK generates phosphoenolpyruvate (PEP) for CO_2 fixation. Supports photosynthetic activity under low availability of CO_2 and regulates energy balance.	Improves drought resistance, enhances photosynthesis productivity and yield.	Zang et al., 2014
Genes, encoding phytohormones				
IPT *(Agrobacterium tumefaciens)*	isopentenyl transferase (IPT)	Synthesis of cytokinins. Support for the stability of cellular structures, control of growth and development.	Improved drought resistance, slower aging, higher yield of grain.	Beznec et al., 2021
Genes, encoding proteins-receptors				
TaPYL4 *(Triticum aestivum)*	Protein (PYRABATIN RESISTANCE	ABA receptor, regulates airway closing.	Smaller airway opening and water loss. Higher efficiency of photosynthesis and grain yield.	Mega et al., 2019

	1-LIKE), (PYL)			
Regulatory genes				
Transcription factors				
DREB/CBF				
AtDREB1A *(Arabidopsis thaliana)*	protein (DEHYDRATION RESPONSIVE ELEMENT BINDING, DREB)	Activates the expression of genes, controlling resistance to low temperatures. Related to the regulation of sugar content, proline, and chlorophyll.	Slower withering, more branched root system, higher total number of spikelets.	Pellegrineschi et al., 2004
			Higher survival rate, higher content of proline.	Wang et al., 2006
			Higher survival in the field, higher velocity and efficiency of water usage.	Saint Pierre et al., 2012
			Higher relative content of water, chlorophyll, sugar, and proline.	Noor et al., 2018
TaDREB1A *(Triticum aestivum)*		Activates the expression of genes, controlling resistance to low temperatures and drought. Supports stability of cell membranes. Supports the increase in the relative content of water, chlorophyll, and soluble sugars.	Higher frequency of seed germination, length of shoots and roots, higher relative content of water, proline, and chlorophyll, higher yield.	Mehmood et al., 2020
TaDREB2, TaDREB3 *(Triticum aestivum)*		*TaDREB2* activates the expression of genes, promoting the adaptation to dehydration and salinization. Regulates water balance and decreases transpiration. *TaDREB3* regulates the expression of genes, responsible for adaptation to low temperatures. Promotes protection of cell	Higher survival rate, slower growth, delayed blossoming, and lower yield of grain	Morran et al., 2011
			Higher survival rate and yield.	Shavrukov et al., 2016

		membranes and improves osmotic regulation.		
GmDREB1 *(Glycine max)*		Activates the expression of genes, promoting the adaptation to dehydration and low temperatures. Supports the stability of cell membranes, regulates the content of soluble sugar, proline, and chlorophyll.	Improved drought resistance, more leaves and roots, and high content of soluble sugar.	Gao et al., 2005
			Higher yield of grain in the field. Lower damage to membranes and improved osmotic adaptation.	Zhou et al., 2020
GhDREB *Gossypium hirsutum*		Activates the expression of genes, promoting the adaptation to drought, salinization, and low temperatures. Regulates the accumulation of soluble sugar, proline, chlorophyll.	Accumulation of soluble sugar, higher chlorophyll content	Gao et al., 2009
TaCBF5L *(Triticum aestivum)*	protein C-REPEAT BINDING FACTOR, CBF	Regulates the expression of genes, controlling drought and frost resistance. Promotes the biosynthesis of osmoprotectors, enhances metabolism of carbohydrates.	Higher total biomass and grain yield.	Yang et al., 2020b
GmTDN1 *(Glycine max)*	DREB-like protein (TOTAL DIGESTIBLE NUTRIENTS, TDN)	Regulates the total amount of digestible nutrients. Improves the efficiency of photosynthetic processes. Promotes the activation of antioxidant enzymes, which decreases ROI rate.	Improved drought resistance, larger plant root mass. Higher yield of grain.	Zhou et al., 2022
TaRAP2.1L mut *(Triticum aestivum)*	modified DREB-like protein (RELATED TO P2.1, *RAP2.1*)	Regulates the activity of genes, related to stress response to drought, water balance and lower oxidative stress.	Enhanced ability to survive under drought, activation of stress-related genes. Higher height of plants, lower grain yield.	Amalraj et al., 2016

ERF				
TaSHN1 *(Triticum aestivum)*	protein SHINE1 (SHN)	Regulates the genes of cuticle biosynthesis, ensures the stability of cell membranes, decreases airway density.	Lower density of airways and water loss, higher accumulation of alkanes.	Bi et al., 2018
TaERF3 *(Triticum aestivum)*	protein (ETHYLENE RESPONSIVE FACTOR, ERF)	Activates the transcription of genes, responding to drought. Affects the decrease in airway opening and decreases transpiration velocity.	Higher survival indices and decreased water loss. Higher accumulation of proline and chlorophyll, lower content of H_2O_2 and airway permeability. Higher rate of ABA and expression of genes, responding to the stress	Rong et al., 2014
WRKY				
TaWRKY2 *(Triticum aestivum)*	protein of WRKY domain	Activates the transcription of genes of osmoprotectors, antioxidants and proteins, stabilizing cell membranes. Promotes lower water loss, support for high photosynthetic activity, decrease in ROI.	Higher survival rate, content of proline, soluble sugars, and chlorophyll. Lower water loss. Higher total biomass, length of panicle, amount, and yield of grain.	Gao et al., 2018
AtWRKY30 *(Arabidopsis thaliana)*		Activates the transcription of genes of antioxidant protection and membrane stabilizers. Promotes the decrease in ROI, supports photosynthetic activity.	Higher biomass, photosynthesis, relative water content, proline, content of soluble proteins and sugars, activity of antioxidant enzymes.	El-Esawi et al., 2019
NAC				
TaNAC69 *(Triticum aestivum)*	protein (NAM/ TAF1-2/ CUC2) (NAC)	Activates genes of response to drought, systems of signal transduction, antioxidant protection. Promotes the accumulation of osmoprotectors, such as soluble sugars and proline.	Higher weight of shoots and roots. Enhanced expression of stress-induced genes.	Xue et al., 2011
OsSNAC1 *(Oriza sativa)*		Activates the expression of genes, responsible for osmoregulation and support for water balance. Participates in	Higher content of water and chlorophyll in leaves, larger fresh and dry biomass.	Saad et al., 2013

		the transmission of auxin signals, supports photosynthetic activity.		
bZIP				
TaABL1 *(Triticum aestivum)*	protein (ABI-LIKE1, ABL1**)**	Activates genes, controlling transpiration and water balance. Participates in closing airways.	Enhanced response to ABA and accelerated closing of airways, higher expression of stress-responsing genes.	Xu et al., 2014
TabZIP2 *(Triticum aestivum)*	protein (BASIC LEUCINE ZIPPER, bZIP**)**	A component of ABA signalling pathway, controls the rebuilding of the flows of carbohydrates and nutrients in response to drought. Enhances the efficiency of water usage, improves photosynthetic activity, decreases ROI level.	Fewer spikelets and kernel, larger weight of a kernel.	Luang et al., 2018
TaFDL2-1A *(Triticum aestivum)*	Protein (FLOWERING DATE-LIKE 2, FDL2)	Activates genes of antioxidants, regulates water balance and stability of cellular membranes. Participates in ABA biosynthesis and removal of ROI.	Higher activity of antioxidant enzymes, higher absorption of ROI.	Wang et al., 2022
HD-Zip				
TaHDZipI-5 ***(Triticum aestivum)***	protein (HOME-ODOMAIN LEUCINE ZIPPER, HDZip)	Regulates the accumulation of osmoprotectors and the activity of antioxidants. Participates in the stabilization of membranes and promotes a decrease in water loss.	Increase drought resistance. Decrease in the size and biomass of plants, delayed blossoming, and decreased grain yield.	Yang et al., 2018
HaHB4 (*Heliánthus ánnuus)*	protein (HOMEOBOX 4, HB4)	Activates the genes, which help retain water and decrease transpiration. Supports the stability of cellular membranes, promotes the accumulation of osmoprotectors, decreases the level of ROI. Inhibits the consumption of ethylene.	Higher efficiency of water usage. Higher number of spikes on a shoot, more shoots and fertile flowers, higher yield.	González et al., 2019

AtHDG11 *(Arabidopsis thaliana)*	protein (HOMEODOMAIN GLOBAROUS 11, HDG11)	Enhances the expression of genes, participating in the ABA synthesis and calcium signalization. Supports photosynthetic activity, decreases the level of ROI. Promotes the growth of roots and decrease in airway density.	Higher yield, higher content of proline, better photosynthesis, lower density of airways, lower velocity of water loss and higher activity of catalase and superoxide dismutase.	Li et al., 2016
ASR				
TaASR1-D *(Triticum aestivum)*	protein (ABSCISIC ACID-STRESS-RIPENING 1), *ASR1*	Regulates the homeostasis of ROI. Stimulates the activity of antioxidant enzymes, which decreases the ROI level. Promotes the decrease in water loss and maintenance of water balance of cells.	Higher indices of survival rate, better ability to retain water. Enhanced antioxidant ability and sensitivity to ABA, lower yield of grain.	Qiu et al., 2021
bHLH				
TabHLH49 *(Triticum aestivum)*	protein (BASIC HELIX-LOOP-HELIX, bHLH)	Regulates the expression of the dehydrin gene *WZY2,* decreasing the water loss via airways and enhancing the osmoregulation. Enhances the activity of antioxidant enzymes, impacts the morphological characteristics of plants.	Better growth, lower content of malondialdehyde, higher relative content of water and chlorophyll.	Liu et al., 2020
BES/BZR				
TaBZR2 *(Triticum aestivum)*	protein (BRASSINAZOLE-RESISTANT 2, BZR2**)**	Participates in the signalization of brassino-steroids. Activates the expression of glutathione-S-transferase-1 to neutralize O_2, enhances photosynthetic activity of plants.	Higher survival rates, higher content of proline, slower leaf roll, lower level of electrolite release, and the content of malondialdehyde.	Cui et al., 2019
NF-Y				
TaNF-YB4 *(Triticum aestivum)*	protein of subunit NF-YB (NUCLEAR	Activates genes of response to water deficit. Regulates the signalling pathways of ABA, growth of roots, shoots, leaves. Promotes the decrease in water loss,	Increase in the number of spikelets in the main spike.	Yadav et al., 2015

	FACTOR GAMMA)	enhances the stability of cellular membranes.		
TaNF-YA7-5B *(Triticum aestivum)*	protein of subunit NF-YA (NUCLEAR FACTOR GAMMA**)**	Activates genes of response to water deficit. Regulates cellular homeostasis of ROI, closing of airways, promotes retaining water in the leaves, activates the genes of osmoprotectors, enhances the photosynthesis efficiency.	Larger length of the shoot and root, biomass. Faster closing of airways and smaller loss of water. Higher content of proline and soluble sugar, lower content of malondialdehyde and ROI. Higher productivity of photosynthesis.	Zhao et al., 2022
MYB				
TaPIMP1 *(Triticum aestivum)*	protein (PIP-TYPE MEMBRANE PROTEINS)	Regulates stress-protective genes in the signalling pathway of ABA - salicylic acid. Maintains water balance and enhances the efficiency of water usage. Promotes the accumulation of osmoprotectors.	Higher efficiency of water usage, survival rates, proline content.	Zhang et al., 2012
TaMpc1-D4 *(Triticum aestivum)*	protein (MYB protein colorless 1, Mpc1)	Regulates drought resistance negatively, decreasing the activity of osmoprotectors and the antioxidant system.	A decrease in expression increased the relative content of water, proline, and the activity of antioxidant enzymes	Li et al., 2020
Proteinkinases				
TaPEPKR2 *(Triticum aestivum)*	protein, related to phosphoenolpyruvate carboxylase, PEPC	Controls metabolism of carbon. Participates in the regulation of metabolism of phosphoenolpyruvate (PEP) and signalling transduction.	Better growth and higher resistance to dehydration, larger total length of the roots.	Zang et al., 2018
TaCIPK19 *(Triticum aestivum)*	protein CBL-I CBL-INTER	Participates in the signalling transduction, mediated by calcium, ROI absorption, and regulation of signalling cascades.	Enhanced ability to absorb ROI.	Wu et al., 2023

TaCIPK23 *(Triticum aestivum)*	ACTING PROTEIN KINASE (CIPK)	Participates in calcium-mediated signalling transduction, airway closing, maintenance of cellular and ion homeostasis, water balance.	Higher percentage of survival, higher content of osmoprotectors, induction of airway closing, enhanced sensitivity to ABA.	Cui et al., 2018
Genes, encoding proteases				
OTS1 *(Arabidopsis thaliana)*	protein of cysteine SUMO protease (OVERLY TOLERANT TO SALT-1)	Post-translation modification of protein. Promotes specific interprotein interactions and stabilizes protein complexes. Regulates the transmission of ABA signals, water balance, aging, protection from ROI.	Delayed aging, higher relative content of water, chlorophyll, and photosynthesis velocity. Lower sumoylation of total proteins.	Le Roux et al., 2019

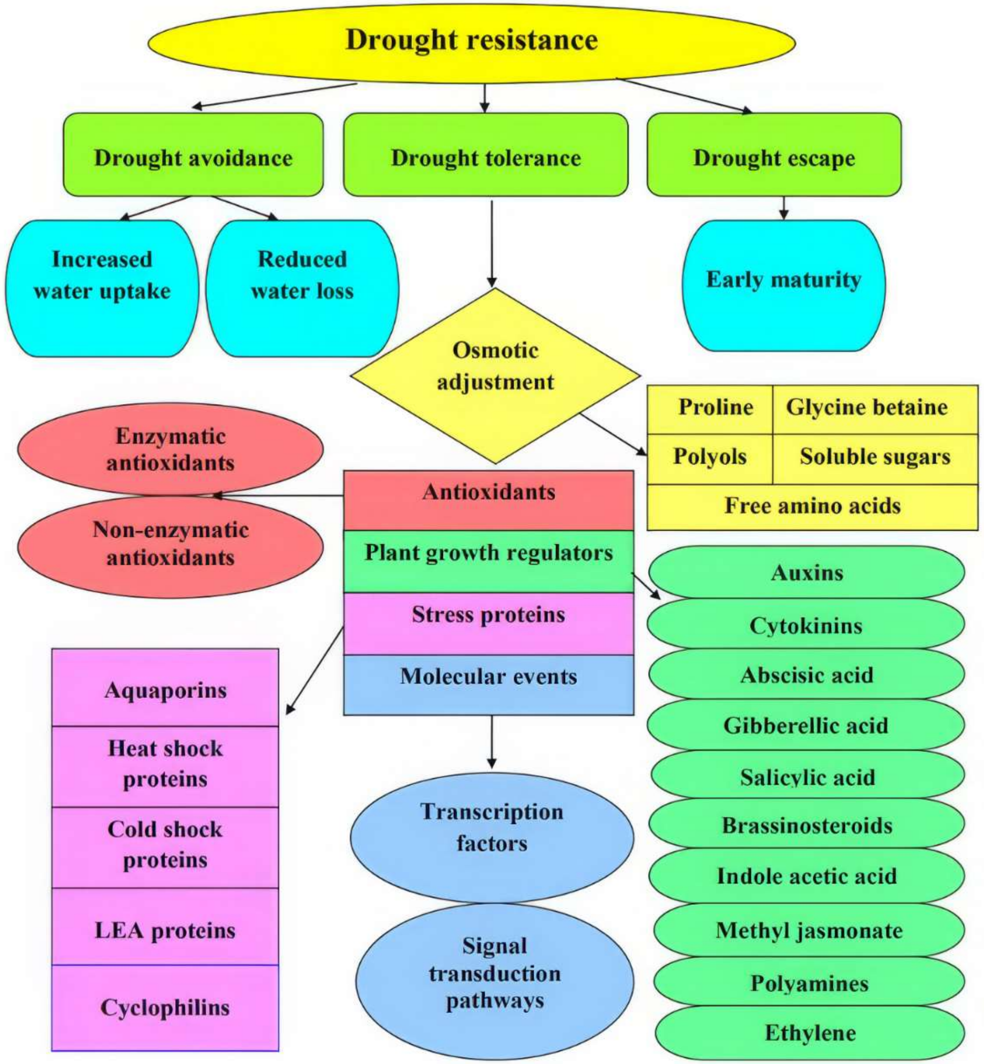

Fig. 1. Mechanisms of plant resistance to drought.

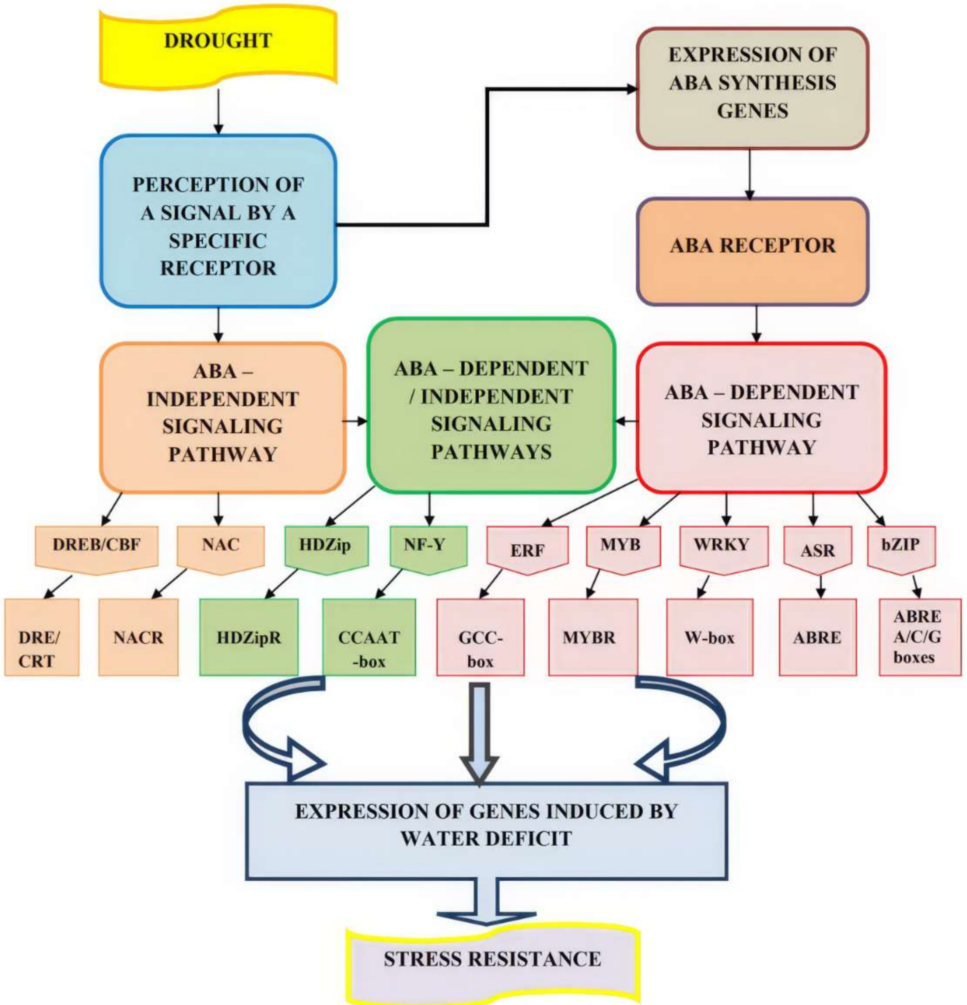

Fig. 2. TFs that function in ABA-dependent and ABA-independent pathways of water deficit response and have been used in the genetic engineering of wheat to improve its drought tolerance.