Supporting Information

Manipulation of oxidative stress responses as a strategy to generate stress-tolerant crops. From damage to signaling to tolerance.

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Table 1. Manipulation of stress tolerance using enzymatic ROS scavengers

Transgene product	Origin	Transgenic plant	Promoter	Stress assayed	Results	References
APX	*Cyanidioschyzon merolae*	Arabidopsis (chloroplast)	CaMV 35S	Heat	Higher pigment contents, lower membrane oxidative damage.	[1]
APX	*Suaeda salsa*	Arabidopsis (chloroplast)	CaMV 35S	High light	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage	[2]
APX	Pea	Tobacco (chloroplast)	CaMV 35S	UVC radiation	Lower membrane oxidative damage, better growth (shoot, root fresh weight and length), higher germination rates	[3]
APX	Eggplant	Rice (cytosol)	Ubiquitin 1	Flood	Higher pigment contents, better growth (coleoptile and root length)	[4]
Cu/ZnSOD	Rice	Rice (chloroplast)	CaMV 35S	Salt	Better growth (height), higher germination rates	[5]
FeSOD	Arabidopsis	Alfalfa (chloroplast)	CaMV 35S	Winter survival	Higher photosynthetic activity	[6]
Cu/ZnSOD	Rubber tree	Rubber tree (cytosol)	CaMV 35S	Drought	Higher photosynthetic activity, better growth (height), increased survival rates	[7]
Cu/ZnSOD	Peanut	Tobacco (cytosol)	CaMV 35S	Drought - Salt	Higher pigment contents, lower membrane oxidative damage, increased germination and survival rates	[8]
Cu/ZnSOD	*Jatropha curcas*	Arabidopsis (cytosol)	CaMV 35S	Salt	Lower membrane oxidative damage, better growth (rosette area, number of leaves, root length), higher germination rates	[9]

MnSOD	Wheat	Canola (mitochondria)	CaMV 35S	Al - Oxidative (MV)	Higher pigment contents, lower membrane oxidative damage, better growth (root length)	[10]
APX - Cu/ZnSOD	Pea - Cassava	Sweet potato (chloroplast)	SWPA2	Chilling	Higher photosynthetic activity	[11]
APX - Cu/ZnSOD	Pea - Cassava	Sweet potato (chloroplast)	SWPA2	Salt	Higher photosynthetic activity and pigment contents, better growth (total fresh weight, root length)	[12]
APX - Cu/ZnSOD	Pea - Spinach	Tobacco (cytosol)	CaMV 35S (2X)	Drought	Higher photosynthetic activity	[13]
APX - Cu/ZnSOD	Pea - Spinach	Plum (cytosol)	CaMV 35S	Salt	Lower membrane oxidative damage	[14]
APX - Cu/ZnSOD	Cassava	Cassava (cytosol)	CaMV 35S - p54/1.0	Chilling	Higher pigment contents, lower membrane oxidative damage.	[15]
APX - Cu/ZnSOD (2X)	Pea - Spinach	Plum (cytosol)	CaMV 35S	Drought	Higher photosynthetic activity, better growth (height, leaf area)	[16]
APX - Cu/ZnSOD - DHAR	Pea - Pea - Human	Tobacco (chloroplast)	CaMV 35S	Salt	Better growth (shoot and root dry weight)	[17]
APX - Cu/ZnSOD - *codA*	Pea - Cassava - *Arthrobacter globiformis*	Potato (chloroplast)	SWPA2	Drought - Salt	Higher photosynthetic activity and pigment contents, better growth (total dry weight)	[18]
APX - Cu/ZnSOD - NDPK2	Pea - Cassava - Arabidopsis	Potato (chloroplast)	SWPA2	Heat	Higher photosynthetic activity, decreased wilting	[19]
Cu/ZnSOD - CAT	Cassava	Cassava (cytosol, peroxisome)	CaMV 35S	Chilling - Drought	Lower membrane oxidative damage	[20]

MnSOD - GR	Tobacco - *Escherichia coli*	Tobacco (chloroplast)	Prrn	Photooxidation - UVB radiation	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage	[21]
MDHAR	Arabidopsis	Tobacco (cytosol)	CaMV 35S	Salt - Osmotic - Oxidative (ozone)	Higher photosynthetic activity	[22]
DHAR	Arabidopsis	Arabidopsis (mitochondria)	CaMV 35S (2X)	Heat - High light	Higher pigment contents, lower membrane oxidative damage.	[23]
DHAR	Arabidopsis	Potato (cytosol)	CaMV 35S (2X)	Drought - Salt - Oxidative (MV)	Higher pigment contents, lower membrane oxidative damage, better growth (shoot length)	[24]
MDHAR - DHAR	*Brassica rapa*	Arabidopsis (cytosol)	SWPA2	Freezing	Higher pigment contents, better growth (fresh weight), higher survival rate	[25]
DHAR - GR	Rice - *E. coli*	Tobacco (chloroplast)	Prrn	Chilling - Salt	Higher photosynthetic activity and pigment contents, better growth rates	[26]
GR	*E. coli*	*Populus tremula x Populus alba* (chloroplast and cytosol)	CaMV 35S (2X)	Photoinhibition - Oxidative (MV)	Higher photosynthetic activity	[27]
GST	Pear	Tobacco (cytosol)	CaMV 35S	Drought - Salt	Lower membrane oxidative damage, higher survival rates	[28]
Tau GST	Orange	Tobacco (cytosol)	CaMV 35S	Osmotic - Salt	Better growth (root length)	[29]
GST - GR	*E. coli*	Tobacco (chloroplast)	Prrn	Chilling - Salt	Higher photosynthetic activity and pigment contents, better growth rates	[26]
CAT1	Wheat	Arabidopsis (peroxisome)	CaMV 35S	Osmotic - Salt - Oxidative (H_2O_2)	Better growth (leaf area, fresh weight)	[30]
CAT1 - GST	*Suaeda salsa*	Rice (NR)	CaMV 35S	Cd - Heat	Higher pigment contents, lower membrane oxidative damage,	[31]

					better growth (shoot fresh and dry weight)	
GPX	Mouse	Tomato (cytosol, apoplast)	CaMV 35S	Mechanical	Better growth (stem length)	[32]
Prx	Arabidopsis	Tall fescue (chloroplast)	CaMV 35S	Heat	Higher photosynthetic activity, lower membrane oxidative damage	[33]
Prx	Arabidopsis	Potato (chloroplast)	SWPA2, CaMV 35S	Heat	Higher photosynthetic activity	[34]
AKR1	Rice	Tobacco (cytosol)	CaMV 35S	Heat	Higher photosynthetic activity, lower membrane oxidative damage	[35]
AKR1	*Pseudomonas spp.*	Rice, tobacco (cytosol)	Rubisco small subunit	Induced ageing - Seed deterioration	Increased seed viability and vigor	[36]
ALDH	Arabidopsis	Arabidopsis (chloroplast)	CaMV 35S	Drought - Salt	Lower membrane oxidative damage	[37]
ALDH 2B8	Grapevine	Arabidopsis (mitochondria)	CaMV 35S	Salt	Higher pigment contents, lower membrane oxidative damage, better growth (root length)	[38]
ALDH 12A1	*Cleistogenes songorica*	Alfalfa (mitochondria)	CaMV 35S	Drought - Salt	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage, better growth (total height and fresh weight)	[39]
Glyoxalases I and II	*Brassica juncea* - *Pennisetum glaucum*	Tomato (cytosol)	CaMV 35S	Salt	Higher pigment contents, lower membrane oxidative damage, increased survival rates	[40]

Abbreviations: 2X: double copy of the gene or promoter; AKR1: aldo-keto reductase 1; ALDH: aldehyde dehydrogenase; APX: ascorbate peroxidase; CaMV 35S: cauliflower mosaic virus 35S promoter; CAT: catalase; *codA*, gene encoding choline oxidase; DHAR: dehydroascorbate reductase; GPX: glutathione peroxidase; GR: glutathione reductase; GST: glutathione *S*-transferase; MDHAR: monodehydroascorbate reductase; MV: methyl viologen; NDPK2: nucleoside diphosphate kinase; p54/1.0: vascular promoter; Prrn: constitutive 16S rRNA promoter; Prx: 2-Cys peroxiredoxin; Rubisco: ribulose 1,5-bisphosphate carboxylase/oxigenase; SOD: superoxide dismutase; SWPA2: sweet potato peroxidase promoter; NR: not reported. Parentheses in the Transgenic plant column indicate the location where the transgenic product was targeted.

Table 2. Stress tolerance of genetically modified plants with altered levels of non-enzymatic ROS scavengers

Transgene product	Compound	Origin	Transgenic plant	Promoter	Stress assayed	Results	References
GDP-mannose 3', 5'-epimerase	ASC	Tomato	Tomato (cytosol)	CaMV 35S	Chilling - Salt Oxidative (MV)	Higher pigment contents, lower membrane oxidative damage, better growth (total fresh weight, root length), increased survival and germination rates	[41]
GalUR	ASC	Strawberry	Potato (cytosol)	CaMV 35S	Salt	Better growth (total height)	[42]
GalUR	ASC	Strawberry	Tomato (cytosol)	CaMV 35S	Chilling - Salt	Higher pigment contents, lower membrane oxidative damage, better growth (total fresh weight), increased survival rates	[43]
Myoinositol oxygenase-L-gulono-1,4-lactone oxidase	ASC	Rat - Arabidopsis	Arabidopsis (cytosol)	CaMV 35S	Chilling - Heat - Salt	Reduced pigment contents, better growth (rosette diameter, inflorescence height, total dry weight), higher germination rates	[44]
Phosphomannose isomerase I	ASC	*Brassica campestris*	Tobacco (cytosol)	CaMV 35S	Salt	Higher germination rates	[45]
OxR	ASC	Arabidopsis	Arabidopsis (ER)	CaMV 35S	Osmotic - Salt - Oxidative (H_2O_2)	Better growth (root length)	[46]
GS	Glutathione	*E. coli*	*Populus tremula x Populus alba* (cytosol)	CaMV 35S (2X)	Photoinhibition - Oxidative (MV)	Lower photosynthetic activity	[27]
GS	Glutathione	Rice	Rice	Cc1	Oxidative (MV) – Natural paddy field conditions	Lower membrane oxidative damage. Improved grain yield and biomass in paddy field	[47]

γGCL	Glutathione	*E. coli*	Tobacco (chloroplast)	CaMV 35S (2X)	High light	Lower photosynthetic activity	[48]
γGCL	Glutathione	Arabidopsis	Arabidopsis (chloroplast)	rd29	Drought - Salt	Better growth (root length), higher germination rates, increased survival rates	[49]
γGCL	Gluathione	*Brassica juncea*	Rice	Rab21	Oxidative (MV).-.Salt	Lower membrane oxidative damage, higher chlorophyll-fluorescence. Increased grain yield in paddy field	[50]
γGCL	Gluathione	Rice	Rice	Rab21	Oxidative (MV).-.Salt	Lower membrane oxidative damage, higher chlorophyll-fluorescence, better germination rates. Improved biomass in paddy field	[51]
γGCL-GS	Glutathione	*Streptococcus thermophilus*	Tobacco (chloroplast and cytosol)	CaMV 35S	Oxidative (MV)	Lower membrane oxidative damage, better growth rates	[52]
γ-Tocopherol methyltransferase	α-Tocopherol	Arabidopsis	*Brassica juncea* (chloroplast)	CaMV 35S	Osmotic - Salt	Reduced membrane oxidative damage	[53]
Prephenate dehydrogenase - Hydroxyphenyl pyruvate dioxygenase	Tocotrienol	Yeast - Arabidopsis	Tobacco (chloroplast)	H4748	Chilling - High light	Higher photosynthetic activity, reduced membrane oxidative damage	[54]
β-Carotene ketolase	Ketocarotenoids	*Haematococcus pluvialis*	Carrot (chloroplast)	CaMV 35S	UVB radiation	Higher pigment contents, better growth (total fresh weight), decreased wilting	[55]
β-Carotene hydroxylase 1	Carotenoids	Mulberry	Mulberry (chloroplast)	CaMV 35S	Drought - Heat - Osmotic - Salt	Higher photosynthetic activity and pigment contents, reduced membrane oxidative damage	[56]

Carotenoid cleavage dioxygenase	Carotenoids	Saffron	Arabidopsis (ER)	CaMV 35S	Osmotic - Salt	Better growth (root length, total fresh weight), increased survival rates	[57]
Lycopene ciclase	Lycopene	*Salicornia europea*	Arabidopsis - *Nicotiana benthamiana* (chloroplast)	CaMV 35S	Salt	Higher photosynthetic activity and pigment contents, increased survival rates	[58]
Isoflavone reductase-like gene	Flavonoids	Rice	Rice (chloroplast)	AIPC	Oxidative (MV)	Higher photosynthetic activity, reduced chlorosis	[59]
Flavanone 3-hydroxilase	Flavonoids	*Lycium chinense*	Tobacco (ER, cytosol)	CaMV 35S	Drought	Higher photosynthetic activity, lower membrane oxidative damage	[60]
Pyridoxine oxidases 1 and 2	Vitamin B6	Arabidopsis	Arabidopsis (cytosol)	CaMV 35S	Oxidative (MV, $^1O_2$)	Lower membrane oxidative damage, better growth (leaf area), higher germination rates	[61]
Isoprene synthase	Isoprene	White poplar	Tobacco (plastids)	CaMV 35S	Heat - Oxidative (ozone)	Higher photosynthetic activity	[62]
N-Acetylserotonin O-methyltransferase	Melatonin	*Malus zumi*	Arabidopsis (cytosol)	CaMV 35S	Drought	Lower membrane oxidative damage, better growth (total fresh weight, lateral root numbers)	[63]
Serotonin N-acetyltransferase	Melatonin	*M. zumi*	Arabidopsis (mitochondria)	CaMV 35S	Drought	Better growth (total fresh weight, lateral root numbers)	[64]
P5CS	Proline	Moth bean	Wheat (cytosol)	AIPC	Drought	Higher photosynthetic activity, lower membrane oxidative damage	[65]
P5CS	Proline	Moth bean	Swingle citrumelo (cytosol)	CaMV 35S	Drought	Higher photosynthetic activity	[66]

P5CS	Proline	Moth bean	Sugarcane (cytosol)	AIPC	Salt	Higher photosynthetic activity, lower membrane oxidative damage	[67]
codA	Glycinebetaine	*Arthrobacter globiformis*	Potato (chloroplast)	SWPA2	Drought - Salt	Higher photosynthetic activity, better growth (total fresh weight)	[68]
codA	Glycinebetaine	*A. globiformis*	Potato (chloroplast)	SWPA2	Drought	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage	[69]
codA	Glycinebetaine	*A. globiformis*	Alfalfa (chloroplast)	SWPA2	Drought - Salt	Higher pigment contents, lower membrane oxidative damage, increased survival rates	[70]
codA	Glycinebetaine	*A. globiformis*	Sweet potato (chloroplast)	SWPA2	Drought	Lower membrane oxidative damage	[71]
codA	Glycinebetaine	*A. globiformis*	Poplar (chloroplast)	SWPA2	Chilling - Drought - Salt	Higher photosynthetic activity, lower membrane oxidative damage	[72]
TPSP	Trehalose	*E. coli*	Rice (cytosol)	Ubiquitin 1	Chilling - Drought - Salt	Higher photosynthetic activity, better growth (root and shoot length), increased survival rates	[73]
TPSP	Trehalose	Yeast	Arabidopsis (cytosol)	CaMV 35S - rd29A	Drought - Freezing - Heat - Salt	Increased survival rates	[74]
Galactinol synthases 1 and 2	Galactinol, raffinose	Arabidopsis	Arabidopsis (cytosol)	CaMV 35S	Chilling - Salt	Higher photosynthetic activity, lower membrane oxidative damage	[75]

Abbreviations: 2X: double copy of the gene or promoter; ABA: abscisic acid; AIPC: ABA-inducible promoter; ASC: ascorbate; *codA*: gene encoding choline oxidase; CaMV 35S: cauliflower mosaic virus 35S promoter; Cc1: cytochrome c promoter; ER: endoplasmic reticulum; GalUR: d-galacturonic acid reductase; γGCL: γ-glutamylcysteinyl ligase; γGCL-GS: bifunctional γ-glutamylcysteinyl ligase-glutathione synthetase enzyme; GS: glutathione synthetase; H4748: duplicated promoter from the Arabidopsis histone gene; MV: methyl viologen; OxR: stress-responsive gene; P5CS: Δ1-pyrroline-5-carboxylate synthetase; Rab21: stress-inducible promoter; rd29: stress-inducible promoter; SWPA2: stress-inducible peroxidase promoter; TPSP: trehalose-6-phosphate synthase–trehalose-6-phosphatase. Parentheses in the Transgenic plant column indicate the location where the transgenic product was targeted.

Table 3. Engineering stress tolerance by manipulating dissipative and avoidance mechanisms

Transgene product	Origin	Transgenic plant	Promoter	Stress assayed	Results	References
PTOX	Arabidopsis	Tobacco (chloroplast)	CaMV 35S (2X)	High light - Low light	Decreased photosynthetic activity	[76]
AOX	Rice	Rice (mitochondria)	Ubiquitin 1	Heat	Better growth (shoot length)	[77]
AOX	Tobacco	Tobacco (mitochondria)	CaMV 35S	Drought	Higher photosynthetic activity	[78]
UCP	Tomato	Tomato (mitochondria)	CaMV 35S	Heat	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage, better growth (dry and fresh weight)	[79]
GOX	Rice	Rice (peroxisome)	CaMV 35S	Heat - High light	Higher photosynthetic activity	[80]
Glyoxylate aminotransferase	Arabidopsis	*Lemna minor* (peroxisome)	CaMV 35S	Salt	Higher photosynthetic activity, lower membrane oxidative damage	[81]
Fld	*Anabaena* PCC 7119	Tobacco (chloroplast)	CaMV 35S	Chilling - Drought - Heat - High light	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage, reduced leaf bleaching	[82, 83]
Fld	*Anabaena* PCC 7119	*Agrostis stolonifera* (chloroplast)	CaMV 35S	Drought - Heat - Nitrogen starvation	Higher pigment contents, lower membrane oxidative damage, higher nitrogen content	[84]
FNR	Pea	Tobacco (chloroplast)	CaMV 35S	Chilling - High light	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage	[85]
FNR - Fld	*Anabaena* PCC 7119	Tobacco (chloroplast)	CaMV 35S	Oxidative stress (MV)	Higher photosynthetic activity, lower membrane	[86, 87]

					oxidative damage and ROS accumulation	
MDH	Apple	Apple (cytosol)	CaMV 35S	Chilling - Salt	Higher photosynthetic activity	[88]
MDH	Maize	Arabidopsis (chloroplast)	CaMV 35S	Salt	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage, better growth (total fresh and dry weight)	[89]
Ferritin	Alfalfa	Tobacco (chloroplast)	Rubisco small subunit	Chilling	Higher photosynthetic activity and pigment contents	[90]
Ferritin	Wheat	Wheat (chloroplast)	Ubiquitin 1	Heat	Higher photosynthetic activity, lower membrane oxidative damage	[91]
Ferritin	Banana	Banana (chloroplast)	CaMV 35S	Excess iron	Higher photosynthetic activity, lower membrane oxidative damage	[92]
Fe-chelatase	*Bradyrhizobium japonicum*	Rice (cytosol)	Ubiquitin 1	Osmotic - Salt	Higher photosynthetic activity and pigments contents, lower membrane oxidative damage	[93]
Solanesyl diphosphate synthase	Arabidopsis	Arabidopsis (ER)	CaMV 35S	High light	Higher photosynthetic activity, lower membrane oxidative damage	[94]

Abbreviations: 2X: double copy of the gene or promoter; AOX: mitochondrial alternative oxidase; CaMV 35S: cauliflower mosaic virus 35S promoter; ER: endoplasmic reticulum; Fld: flavodoxin; FNR: ferredoxin-NADP(H) oxidoreductase; GOX: glycolate oxidase; MDH: NADPH-dependent malate dehydrogenase; MV: methyl viologen; PTOX: plastid terminal oxidase; Rubisco: ribulose 1,5-bisphosphate carboxylase/oxygenase; UCP: mitochondrial uncoupling protein. Parentheses in the Transgenic plant column indicate the location where the transgenic product was targeted.

Table 4. Improving stress tolerance by engineering reductive repair systems

Transgene product	Origin	Transgenic plant	Promoter	Stress assayed	Results	References
Trx H	Tobacco	Tobacco (chloroplast)	PPP1	Oxidative (MV)	Lower ROS accumulation	[95]
Trx F, Trx M	Tobacco	Tobacco (chloroplast)	Prrn, PrrnG10L, PpsbA	Chilling - High light - Oxidative (MV)	Higher photosynthetic activity and pigments contents, lower membrane oxidative damage	[96]
Trx M2	Arabidopsis	Arabidopsis (chloroplast)	CaMV 35S	Salt	Better growth (total fresh weight, root length)	[97]
NTR	Arabidopsis	Arabidopsis (cytosol)	CaMV 35S	Drought	Higher pigment contents, better growth (total fresh weight), increased survival rates	[98]
Grx 5	*Pteris vittata*	Arabidopsis (plastid)	mFiMV	Heat	Lower membrane oxidative damage	[99]
Grx S17	Arabidopsis	Tomato (cytosol)	CaMV 35S	Heat	Higher photosynthetic activity and pigment contents, lower membrane oxidative damage, better growth (total fresh and dry weight)	[100]
MSR A4.1	Rice	Rice (chloroplast)	Actin 1	Salt	Higher photosynthetic activity, lower membrane oxidative damage, decreased wilting	[101]
MSR A4	Arabidopsis	Arabidopsis (chloroplast)	CaMV 35S	Osmotic - Salt	Better growth (root length)	[102]
MSR B2	Pepper	Tomato (cytosol)	CaMV 35S	Oxidative (MV)	Higher pigment contents, lower membrane oxidative damage	[103]

Abbreviations: CaMV 35S: cauliflower mosaic virus 35S promoter; mFiMV: fig mosaic virus promoter; Grx: glutaredoxin; MSR: methionine sulfoxide reductases; MV: methyl viologen; NTR: NADPH-dependent thioredoxin reductase; PpsbA: constitutive chloroplast promoter; PPP1: pathogen-inducible promoter; Prrn: constitutive 16S rRNA

promoter; PrrnG10L: Prrn fused to the leader region of the bacteriophage T7 gene 10; Trx: thioredoxin. Parentheses in the Transgenic plant column indicate the location where the transgenic product was targeted.

References:

1. Hirooka S, Misumi O, Yoshida M, et al. Expression of the *Cyanidioschyzon merolae* stromal ascorbate peroxidase in *Arabidopsis thaliana* enhances thermotolerance. Plant Cell Rep. 2009;28:1881-93.
2. Pang CH, Li K, Wang B. Overexpression of SsCHLAPXs confers protection against oxidative stress induced by high light in transgenic *Arabidopsis thaliana*. Physiol Plant. 2011;143:355-66.
3. Saxena S, Joshi P, Grimm B, et al. Alleviation of ultraviolet-C-induced oxidative damage through overexpression of cytosolic ascorbate peroxidase. Biologia. 2011;66. doi: 10.2478/s11756-011-0120-4.
4. Chiang CM, Chen LFO, Shih SW, et al. Expression of eggplant ascorbate peroxidase increases the tolerance of transgenic rice plants to flooding stress. J Plant Biochem Biotech. 2014;24:257-267.
5. Guan Q, Liao X, He M, et al. Tolerance analysis of chloroplast OsCu/Zn-SOD overexpressing rice under NaCl and $NaHCO_3$ stress. PLoS One. 2017;12:e0186052. doi: 10.1371/journal.pone.0186052.
6. McKersie BD, Murnaghan J, Jones KS, et al. Iron-superoxide dismutase expression in transgenic alfalfa increases winter survival without a detectable increase in photosynthetic oxidative stress tolerance. Plant Physiol. 2000;122:1427-1438.
7. Leclercq J, Martin F, Sanier C, et al. Over-expression of a cytosolic isoform of the HbCuZnSOD gene in *Hevea brasiliensis* changes its response to a water deficit. Plant Mol Biol. 2012;80:255-72.
8. Negi NP, Shrivastava DC, Sharma V, et al. Overexpression of CuZnSOD from *Arachis hypogaea* alleviates salinity and drought stress in tobacco. Plant Cell Rep. 2015;34:1109-26.
9. Liu ZB, Zhang WJ, Gong XD, et al. A Cu/Zn superoxide dismutase from *Jatropha curcas* enhances salt tolerance of *Arabidopsis thaliana*. Genet Mol Res. 2015;14:2086-98.
10. Basu U, Good A, Taylor G. Transgenic *Brassica napus* plants overexpressing aluminium-induced mitochondrial manganese superoxide dismutase cDNA are resistant to aluminium. Plant Cell Environ. 2001;24:1278-1269.
11. Lim S, Kim Y-H, Kim S-H, et al. Enhanced tolerance of transgenic sweet potato plants that express both CuZnSOD and APX in chloroplasts to methyl viologen-mediated oxidative stress and chilling. Mol Breed. 2007;19:227-239.
12. Yan H, Li Q, Park SC, et al. Overexpression of CuZnSOD and APX enhance salt stress tolerance in sweet potato. Plant Physiol Biochem. 2016;109:20-27.
13. Faize M, Burgos L, Faize L, et al. Involvement of cytosolic ascorbate peroxidase and Cu/Zn-superoxide dismutase for improved tolerance against drought stress. J Exp Bot. 2011;62:2599-613.
14. Diaz-Vivancos P, Faize M, Barba-Espin G, et al. Ectopic expression of cytosolic superoxide dismutase and ascorbate peroxidase leads to salt stress tolerance in transgenic plums. Plant Biotech J. 2013;11:976-85.
15. Xu J, Yang J, Duan X, et al. Increased expression of native cytosolic Cu/Zn superoxide dismutase and ascorbate peroxidase improves tolerance to oxidative and

chilling stresses in cassava (*Manihot esculenta* Crantz). BMC Plant Biol. 2014;14:208.
16. Diaz-Vivancos P, Faize L, Nicolas E, et al. Transformation of plum plants with a cytosolic ascorbate peroxidase transgene leads to enhanced water stress tolerance. Ann Bot. 2016;117:1121-1131.
17. Lee YP, Kim SH, Bang JW, et al. Enhanced tolerance to oxidative stress in transgenic tobacco plants expressing three antioxidant enzymes in chloroplasts. Plant Cell Rep. 2007;26:591-598.
18. Ahmad R, Kim YH, Kim MD, et al. Simultaneous expression of choline oxidase, superoxide dismutase and ascorbate peroxidase in potato plant chloroplasts provides synergistically enhanced protection against various abiotic stresses. Physiol Plant. 2010;138:520-33.
19. Kim MD, Kim YH, Kwon SY, et al. Enhanced tolerance to methyl viologen-induced oxidative stress and high temperature in transgenic potato plants overexpressing the CuZnSOD, APX and NDPK2 genes. Physiol Plant. 2010;140:153-62.
20. Xu J, Duan X, Yang J, et al. Coupled expression of Cu/Zn-superoxide dismutase and catalase in cassava improves tolerance against cold and drought stresses. Plant Signal Behav. 2013;8:e24525. doi: 10.4161/psb.24525.
21. Poage M, Le Martret B, Jansen MA, et al. Modification of reactive oxygen species scavenging capacity of chloroplasts through plastid transformation. Plant Mol Biol. 2011;76:371-84.
22. Eltayeb AE, Kawano N, Badawi GH, et al. Overexpression of monodehydroascorbate reductase in transgenic tobacco confers enhanced tolerance to ozone, salt and polyethylene glycol stresses. Planta. 2007;225:1255-1264.
23. Wang Z, Xiao Y, Chen W, et al. Increased vitamin C content accompanied by an enhanced recycling pathway confers oxidative stress tolerance in Arabidopsis. J Int Plant Biol. 2010;52:400-9.
24. Eltayeb AE, Yamamoto S, Habora MEE, et al. Transgenic potato overexpressing Arabidopsis cytosolic AtDHAR1 showed higher tolerance to herbicide, drought and salt stresses. Breed Sci. 2011;61:3-10.
25. Shin S-Y, Kim M-H, Kim Y-H, et al. Co-expression of monodehydroascorbate reductase and dehydroascorbate reductase from *Brassica rapa* effectively confers tolerance to freezing-induced oxidative stress. Mol Cells. 2013;36:304-315.
26. Le Martret B, Poage M, Shiel K, et al. Tobacco chloroplast transformants expressing genes encoding dehydroascorbate reductase, glutathione reductase, and glutathione-*S*-transferase, exhibit altered anti-oxidant metabolism and improved abiotic stress tolerance. Plant Biotechnol J. 2011;9:661-673.
27. Foyer CH, Souriau N, Perret S, et al. Overexpression of glutathione reductase but not glutathione synthetase leads to increases in antioxidant capacity and resistance to photoinhibition in poplar trees. Plant Physiol. 1995;109:1047-1057.
28. Liu D, Liu Y, Rao J, et al. Overexpression of the glutathione S-transferase gene from *Pyrus pyrifolia* fruit improves tolerance to abiotic stress in transgenic tobacco plants. Mol Biol. 2013;47:515-523.
29. Lo Cicero L, Madesis P, Tsaftaris A, et al. Tobacco plants over-expressing the sweet orange tau glutathione transferases (CsGSTUs) acquire tolerance to the

diphenyl ether herbicide fluorodifen and to salt and drought stresses. Phytochem. 2015;116:69-77.
30. Feki K, Kamoun Y, Mahmoud RB, et al. Multiple abiotic stress tolerance of the transformants yeast cells and the transgenic Arabidopsis plants expressing a novel durum wheat catalase. Plant Physiol Biochem. 2015;97:420-431.
31. Zhao FY, Liu W, Zhang SY. Different responses of plant growth and antioxidant system to the combination of cadmium and heat stress in transgenic and non-transgenic rice. J Int Plant Biol. 2009;51:942-950.
32. Herbette S, de Labrouhe DT, Drevet JR, et al. Transgenic tomatoes showing higher glutathione peroxidase antioxidant activity are more resistant to an abiotic stress but more susceptible to biotic stresses. Plant Sci. 2011;180:548-553.
33. Kim KH, Alam I, Lee KW, et al. Enhanced tolerance of transgenic tall fescue plants overexpressing 2-Cys peroxiredoxin against methyl viologen and heat stresses. Biotechnol Lett. 2010;32:571-576.
34. Kim MD, Kim YH, Kwon SY, et al. Overexpression of 2-cysteine peroxiredoxin enhances tolerance to methyl viologen-mediated oxidative stress and high temperature in potato plants. Plant Physiol Biochem. 2011;49:891-897.
35. Turoczy Z, Kis P, Torok K, et al. Overproduction of a rice aldo-keto reductase increases oxidative and heat stress tolerance by malondialdehyde and methylglyoxal detoxification. Plant Mol Biol. 2011;75:399-412.
36. Nisarga KN, Vemanna RS, Kodekallu Chandrashekar B, et al. Aldo-ketoreductase 1 (AKR1) improves seed longevity in tobacco and rice by detoxifying reactive cytotoxic compounds generated during ageing. Rice (NY). 2017;10:11. doi: 10.1186/s12284-017-0148-3.
37. Sunkar R, Bartels D, Kirch HH. Overexpression of a stress-inducible aldehyde dehydrogenase gene from *Arabidopsis thaliana* in transgenic plants improves stress tolerance. Plant J. 2003;35:452-464.
38. Xu X, Guo R, Cheng C, et al. Overexpression of ALDH2B8, an aldehyde dehydrogenase gene from grapevine, sustains Arabidopsis growth upon salt stress and protects plants against oxidative stress. Plant Cell Tissue Organ Cult. 2013;114:187-196.
39. Duan Z, Zhang D, Zhang J, et al. Co-transforming bar and CsALDH genes enhanced resistance to herbicide and drought and salt stress in transgenic alfalfa (*Medicago sativa* L.). Front Plant Sci. 2015;6:1115. doi: 10.3389/fpls.2015.01115.
40. Alvarez Viveros MF, Inostroza-Blancheteau C, Timmermann T, et al. Overexpression of GlyI and GlyII genes in transgenic tomato (*Solanum lycopersicum* Mill.) plants confers salt tolerance by decreasing oxidative stress. Mol Biol Rep. 2013;40:3281-90.
41. Zhang C, Liu J, Zhang Y, et al. Overexpression of SlGMEs leads to ascorbate accumulation with enhanced oxidative stress, cold, and salt tolerance in tomato. Plant Cell Rep. 2011;30:389-398.
42. Upadhyaya CP, Venkatesh J, Gururani MA, et al. Transgenic potato overproducing L-ascorbic acid resisted an increase in methylglyoxal under salinity stress via maintaining higher reduced glutathione level and glyoxalase enzyme activity. Biotechnol Lett. 2011;33:2297-2307.

43. Cai X, Zhang C, Ye J, et al. Ectopic expression of FaGalUR leads to ascorbate accumulation with enhanced oxidative stress, cold, and salt tolerance in tomato. Plant Growth Reg. 2014;76:187-197.
44. Lisko KA, Torres R, Harris RS, et al. Elevating vitamin C content via overexpression of myo-inositol oxygenase and l-gulono-1,4-lactone oxidase in Arabidopsis leads to enhanced biomass and tolerance to abiotic stresses. In Vitro Cell Dev Biol Plant. 2013;49:643-655.
45. Wang X, Zhang S, Hu D, et al. BcPMI2, isolated from non-heading Chinese cabbage encoding phosphomannose isomerase, improves stress tolerance in transgenic tobacco. Mol Biol Rep. 2014;41:2207-2216.
46. Bu Y, Sun B, Zhou A, et al. Overexpression of *AtOxR* gene improves abiotic stresses tolerance and vitamin C content in *Arabidopsis thaliana*. BMC Biotech. 2016;16:69.
47. Park S-I, Kim Y-S, Kim J-J, et al. Improved stress tolerance and productivity in transgenic rice plants constitutively expressing the *Oryza sativa* glutathione synthetase OsGS under paddy field conditions. J Plant Physiol. 2017;215:39-47.
48. Creissen G, Firmin J, Fryer M, et al. Elevated glutathione biosynthetic capacity in the chloroplasts of transgenic tobacco plants paradoxically causes increased oxidative stress. Plant Cell. 1999;11:1277-1291.
49. Cheng MC, Ko K, Chang WL, et al. Increased glutathione contributes to stress tolerance and global translational changes in Arabidopsis. Plant J. 2015;83:926-939.
50. Bae M-J, Kim Y-S, Kim I-S, et al. Transgenic rice overexpressing the *Brassica juncea* gamma-glutamylcysteine synthetase gene enhances tolerance to abiotic stress and improves grain yield under paddy field conditions. Mol Breed. 2013;31:931-945.
51. Choe Y-H, Kim Y-S, Kim I-S, et al. Homologous expression of γ-glutamylcysteine synthetase increases grain yield and tolerance of transgenic rice plants to environmental stresses. J Plant Physiol. 2013;170:610-618.
51. Liedschulte V, Wachter A, Zhigang A, et al. Exploiting plants for glutathione (GSH) production: uncoupling GSH synthesis from cellular controls results in unprecedented GSH accumulation. Plant Biotech J. 2010;8:807-820.
53. Kumar D, Yusuf MA, Singh P, et al. Modulation of antioxidant machinery in alpha-tocopherol-enriched transgenic *Brassica juncea* plants tolerant to abiotic stress conditions. Protoplasma. 2013;250:1079-1089.
54. Matringe M, Ksas B, Rey P, et al. Tocotrienols, the unsaturated forms of vitamin E, can function as antioxidants and lipid protectors in tobacco leaves. Plant Physiol. 2008;147:764-78.
55. Jayaraj J, Punja ZK. Transgenic carrot plants accumulating ketocarotenoids show tolerance to UV and oxidative stresses. Plant Physiol Biochem. 2008;46:875-883.
56. Saeed B, Das M, Khurana P. Overexpression of β-carotene hydroxylase1 (BCH1) in Indian mulberry, *Morus indica* cv. K2, confers tolerance against UV, high temperature and high irradiance stress induced oxidative damage. Plant Cell Tissue Organ Cult. 2014;120:1003-1014.
57. Baba SA, Jain D, Abbas N, et al. Overexpression of *Crocus* carotenoid cleavage dioxygenase, CsCCD4b, in Arabidopsis imparts tolerance to dehydration, salt and oxidative stresses by modulating ROS machinery. J Plant Physio. 2015;189:114-125.

58. Chen X, Han H, Jiang P, et al. Transformation of beta-lycopene cyclase genes from *Salicornia europaea* and Arabidopsis conferred salt tolerance in Arabidopsis and tobacco. Plant Cell Physiol. 2011;52:909-921.
59. Kim SG, Kim ST, Wang Y, et al. Overexpression of rice isoflavone reductase-like gene (OsIRL) confers tolerance to reactive oxygen species. Physiol Plant. 2010;138:1-9.
60. Song X, Diao J, Ji J, et al. Molecular cloning and identification of a flavanone 3-hydroxylase gene from *Lycium chinense*, and its overexpression enhances drought stress in tobacco. Plant Physiol Biochem. 2016;98:89-100.
61. Raschke M, Boycheva S, Crevecoeur M, et al. Enhanced levels of vitamin B(6) increase aerial organ size and positively affect stress tolerance in Arabidopsis. Plant J. 2011;66:414-432.
62. Vickers CE, Possell M, Cojocariu CI, et al. Isoprene synthesis protects transgenic tobacco plants from oxidative stress. Plant Cell Environ. 2009 May;32:520-31.
63. Zuo B, Zheng X, He P, et al. Overexpression of MzASMT improves melatonin production and enhances drought tolerance in transgenic *Arabidopsis thaliana* plants. J Pineal Res. 2014;57:408-417.
64. Wang L, Feng C, Zheng X, et al. Plant mitochondria synthesize melatonin and enhance the tolerance of plants to drought stress. J Pineal Res. 2017;63. doi: 10.1111/jpi.12429.
65. Vendruscolo EC, Schuster I, Pileggi M, et al. Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. J Plant Physiol. 2007;164:1367-1376.
66. de Campos MKF, de Carvalho K, de Souza FS, et al. Drought tolerance and antioxidant enzymatic activity in transgenic 'Swingle' citrumelo plants over-accumulating proline. Environm Exp Bot. 2011;72:242-250.
67. Guerzoni JTS, Belintani NG, Moreira RMP, et al. Stress-induced Δ1-pyrroline-5-carboxylate synthetase (P5CS) gene confers tolerance to salt stress in transgenic sugarcane. Acta Phys Plant. 2014;36:2309-2319.
68. Ahmad R, Kim MD, Back KH, et al. Stress-induced expression of choline oxidase in potato plant chloroplasts confers enhanced tolerance to oxidative, salt, and drought stresses. Plant Cell Rep. 2008;27:687-698.
69. Cheng Y-J, Deng X-P, Kwak S-S, et al. Enhanced tolerance of transgenic potato plants expressing choline oxidase in chloroplasts against water stress. Bot Stud. 2013;54:30.
70. Li H, Wang Z, Ke Q, et al. Overexpression of *codA* gene confers enhanced tolerance to abiotic stresses in alfalfa. Plant Physiol Biochem. 2014;85:31-40.
71. Park S-C, Kim MD, Kim SH, et al. Enhanced drought and oxidative stress tolerance in transgenic sweet potato expressing a *codA* gene. J Plant Biotech. 2015;42:19-24.
72. Ke Q, Wang Z, Ji CY, et al. Transgenic poplar expressing codA exhibits enhanced growth and abiotic stress tolerance. Plant Physiol Biochem. 2016;100:75-84.
73. Jang IC, Oh SJ, Seo JS, et al. Expression of a bifunctional fusion of the *Escherichia coli* genes for trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase in transgenic rice plants increases trehalose accumulation and abiotic stress tolerance without stunting growth. Plant Physiol. 2003;131:516-24.

74. Miranda JA, Avonce N, Suárez R, et al. A bifunctional TPS-TPP enzyme from yeast confers tolerance to multiple and extreme abiotic-stress conditions in transgenic Arabidopsis. Planta. 2007;226:1411-1421.
75. Nishizawa A, Yabuta Y, Shigeoka S. Galactinol and raffinose constitute a novel function to protect plants from oxidative damage. Plant Physiol. 2008;147:1251-1263.
76. Heyno E, Gross CM, Laureau C, et al. Plastid alternative oxidase (PTOX) promotes oxidative stress when overexpressed in tobacco. J Biol Chem. 2009;284:31174-31180.
77. Murakami Y, Toriyama K. Enhanced high temperature tolerance in transgenic rice seedlings with elevated levels of alternative oxidase, OsAOX1a. Plant Biotech. 2008;25:361-364.
78. Dahal K, Vanlerberghe GC. Alternative oxidase respiration maintains both mitochondrial and chloroplast function during drought. New Phytol. 2017;213:560-571.
79. Chen S, Liu A, Zhang S, et al. Overexpression of mitochondrial uncoupling protein conferred resistance to heat stress and *Botrytis cinerea* infection in tomato. Plant Physiol Biochem. 2013;73:245-253.
80. Cui L-L, Lu Y-s, Li Y, et al. Overexpression of glycolate oxidase confers improved photosynthesis under high light and high temperature in rice. Front Plant Sci. 2016;7:1165.
81. Yang L, Han H, Liu M, et al. Overexpression of the Arabidopsis photorespiratory pathway gene, serine:glyoxylate aminotransferase (*AtAGT1*), leads to salt stress tolerance in transgenic duckweed (*Lemna minor*). Plant Cell Tissue Organ Cult. 2013;113:407-416.
82. Tognetti VB, Palatnik JF, Fillat MF, et al. Stress tolerant plants (EU patent No 02801941.2-2405-GB0204612), European Union, CONICET; 2002.
83. Tognetti VB, Palatnik JF, Fillat MF, et al. Functional replacement of ferredoxin by a cyanobacterial flavodoxin in tobacco confers broad-range stress tolerance. Plant Cell. 2006;18:2035-2050.
84. Li Z, Yuan S, Jia H, et al. Ectopic expression of a cyanobacterial flavodoxin in creeping bentgrass impacts plant development and confers broad abiotic stress tolerance. Plant Biotech J. 2017;15:433-446.
85. Rodriguez RE, Lodeyro A, Poli HO, et al. Transgenic tobacco plants overexpressing chloroplastic ferredoxin-NADP(H) reductase display normal rates of photosynthesis and increased tolerance to oxidative stress. Plant Physiol. 2007;143:639-649.
86. Carrillo N, Giró M, Lodeyro AF, et al. Stress tolerant plants (WO2011018662A1). United States, CONICET. 2011.
87. Giró M, Ceccoli RD, Poli HO, et al. An *in vivo* system involving co-expression of cyanobacterial flavodoxin and ferredoxin–$NADP^+$ reductase confers increased tolerance to oxidative stress in plants. FEBS Open Bio. 2011;1:7-13.
88. Wang QJ, Sun H, Dong QL, et al. The enhancement of tolerance to salt and cold stresses by modifying the redox state and salicylic acid content via the cytosolic malate dehydrogenase gene in transgenic apple plants. Plant Biotech J. 2016;14:1986-1997.

89. Kandoi D, Mohanty S, Tripathy BC. Overexpression of plastidic maize NADP-malate dehydrogenase (ZmNADP-MDH) in *Arabidopsis thaliana* confers tolerance to salt stress. Protoplasma. 2018;255:547-563.
90. Hegedus A, Janda T, Horvath GV, et al. Accumulation of overproduced ferritin in the chloroplast provides protection against photoinhibition induced by low temperature in tobacco plants. J Plant Physiol. 2008 9;165:1647-1651.
91. Zang X, Geng X, Wang F, et al. Overexpression of wheat ferritin gene *TaFER-5B* enhances tolerance to heat stress and other abiotic stresses associated with the ROS scavenging. BMC Plant Biol. 2017 14;17:14.
92. Yadav K, Patel P, Srivastava AK, et al. Overexpression of native ferritin gene *MusaFer1* enhances iron content and oxidative stress tolerance in transgenic banana plants. PLoS One. 2017;12:e0188933. doi: 10.1371/journal.pone.0188933.
93. Kim JG, Back K, Lee HY, et al. Increased expression of Fe-chelatase leads to increased metabolic flux into heme and confers protection against photodynamically induced oxidative stress. Plant Mol Biol. 2014;86:271-287.
94. Ksas B, Becuwe N, Chevalier A, et al. Plant tolerance to excess light energy and photooxidative damage relies on plastoquinone biosynthesis. Sci Rep. 2015;5:10919.92.
95. Sun L, Ren, H, Liu, R, et al. An h-Type thioredoxin functions in tobacco defense responses to two species of viruses and an abiotic oxidative stress. Mol Plant Microbe Interact. 2010;23:1470-1485.
96. Rey P, Sanz-Barrio R, Innocenti G, et al. Overexpression of plastidial thioredoxins f and m differentially alters photosynthetic activity and response to oxidative stress in tobacco plants. Front Plant Sci. 2013;4:390. doi: 10.3389/fpls.2013.00390.
97. Zhang M, Takano T, Liu S, et al. Arabidopsis mitochondrial voltage-dependent anion channel 3 (AtVDAC3) protein interacts with thioredoxin m2. FEBS Lett. 2015;589:1207-13.
98. Cha JY, Kim JY, Jung IJ, et al. NADPH-dependent thioredoxin reductase A (NTRA) confers elevated tolerance to oxidative stress and drought. Plant Physiol Biochem. 2014;80:184-191.96.
99. Sundaram S, Rathinasabapathi B. Transgenic expression of fern *Pteris vittata* glutaredoxin PvGrx5 in *Arabidopsis thaliana* increases plant tolerance to high temperature stress and reduces oxidative damage to proteins. Planta. 2010;231:361-369.
100. Wu Q, Lin J, Liu JZ, et al. Ectopic expression of Arabidopsis glutaredoxin AtGRXS17 enhances thermotolerance in tomato. Plant Biotechnol J. 2012;10:945-55.
101. Guo X, Wu Y, Wang Y, et al. OsMSRA4.1 and OsMSRB1.1, two rice plastidial methionine sulfoxide reductases, are involved in abiotic stress responses. Planta. 2009;230:227-238.
102. Oh JE, Hossain MA, Kim JH, et al. The ectopic expression of methionine sulfoxide reductase 4 results in enhanced growth performance in Arabidopsis. Plant Sci. 2010;178:265-270.
103. Oh SK, Baek KH, Seong ES, et al. CaMsrB2, pepper methionine sulfoxide reductase B2, is a novel defense regulator against oxidative stress and pathogen attack. Plant Physiol. 2010;154:245-261.