Molecular Plant Abiotic Stress

Biology and Biotechnology

Edited by
Aryadeep Roychoudhury
Durgesh Kumar Tripathi

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Dr Aryadeep Roychoudhury
Department of Biotechnology
St. Xavier's College (Autonomous)
30, Mother Teresa Sarani
Kolkata-700016, West Bengal
INDIA

Dr Durgesh Kumar Tripathi
Amity Institute of Organic Agriculture
Amity University Uttar Pradesh
I 2 Block, 5th Floor, AUUP Campus Sector-125
Noida-201313, Uttar Pradesh
INDIA

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List of Contributors

Krishnendu Acharya
Department of Botany
University of Calcutta
Kolkata, West Bengal
India

Nimisha Amist
Plant Physiology Laboratory
Department of Botany
University of Allahabad
Allahabad, 211002
India

Aditi Shreeya Bali
Department of Botany
M.C.M. DAV College for Women
Chandigarh, 160036
India

Aditya Banerjee
Department of Biotechnology
St. Xavier's College (Autonomous)
Kolkata, West Bengal
India

Chanda Bano
Plant Physiology Laboratory
Department of Botany
University of Allahabad
Allahabad, 211002
India

Supratim Basu
NMC Biolab
New Mexico Consortium
Los Alamos, New Mexico
USA

Renu Bhardwaj
Plant Stress Physiology Lab
Department of Botanical &
Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

Deepa Bisht
School of Life Sciences
Jawaharlal Nehru University
New Delhi
India

Dipankar Chakraborti
Department of Biotechnology
St. Xavier's College (Autonomous)
30, Mother Teresa Sarani
Kolkata, 700016, West Bengal
India

Nilanjan Chakraborty
Department of Botany
Scottish Church College
Kolkata, West Bengal
India

Rituparna Kundu Chaudhuri
Department of Botany
Krishnagar Govt. College
Krishnagar, 741101, West Bengal
India

Francinilson Meireles Coelho
Universidade Federal do Pará
Belém, PA
Brazil

Solange da Cunha Ferreira
Universidade Federal do Pará
Belém, PA
Brazil

Prabal Das
Department of Botany
University of Calcutta
Kolkata, West Bengal
India

Sampa Das
Division of Plant Biology
Bose Institute, P1/12, CIT Scheme, VIIM
Kolkata, West Bengal
India

Meenakshi Dua
School of Environmental Sciences
Jawaharlal Nehru University
New Delhi, 110067
India

Shreeparna Ganguly
Department of Biotechnology
St. Xavier's College (Autonomous)
30, Mother Teresa Sarani
Kolkata, 700016, West Bengal
India

Saikat Gantait
Department of Genetics and Plant Breeding
Faculty of Agriculture
Bidhan Chandra Krishi Viswavidyalaya
Mohanpur, Nadia, West Bengal, 741252
India

Budhayash Gautam
Sam Higginbottom University of Agriculture, Technology and Sciences
Allahabad, Uttar Pradesh
India

S. B. Ghag
School of Biological Sciences
UM-DAE Centre for Excellence in Basic Sciences
Kalina campus, Santacruz (East)
Mumbai, Maharashtra
India

Kavita Goswami
International Centre for Genetic Engineering and Biotechnology
New Delhi
India

Sumanti Gupta
Department of Botany
Rabindra Mahavidyalaya
Hooghly, West Bengal
India

Varsha Gupta
National Institute of Plant Genome Research
New Delhi
India

Shokoofeh Hajihashemi
Plant Biology Department
Behbahan Khatam Alanbia University of Technology
Khuzestan
Iran

Abhimanyu Jogawat
National Institute of Plant Genome Research
New Delhi
India

Atul Kumar Johri
School of Life Sciences
Jawaharlal Nehru University
New Delhi
India

Dhriti Kapoor
School of Bioengineering & Biosciences
Lovely Professional University
Punjab, 144411
India

Kavi Kishor PB
Center for Biotechnology
Acharya Nagarjuna University
Guntur, 522510
India

Kanika Khanna
Plant Stress Physiology Lab
Department of Botanical &
Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

Sukhmeen Kaur Kohli
Plant Stress Physiology Lab
Department of Botanical &
Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

Anil Kumar
School of Biotechnology
Shri Mata Vaishno Devi University
Katra, J&K
India

Rakesh Kumar
Department of Botany
DAV University
Sarmastpur, Jalandhar, 144012, Punjab
India

Sandeep Kumar
Department of Environmental Sciences
DAV University
Sarmastpur, Jalandhar, 144012, Punjab
India

Vinod Kumar
Department of Botany
DAV University
Sarmastpur, Jalandhar, 144012, Punjab
India

Maheshwari P
Center for Biotechnology
Acharya Nagarjuna University
Guntur, 522510
India

Sharada Mallubhotla
School of Biotechnology
Faculty of Sciences
Shri Mata Vaishno Devi University
Katra, 182320, J&K
India

Deyvid Novaes Marques
Universidade Federal do Pará
Belém, PA
Brazil

Neeti Sanan-Mishra
International Centre for Genetic
Engineering and Biotechnology
New Delhi
India

Joseph Msanne
NMC Biolab
New Mexico Consortium
Los Alamos, New Mexico
USA

Nikalje GC
Department of Botany
Savitribai Phule Pune University
Pune, 411007
India

Nikam TD
Department of Botany
Savitribai Phule Pune University
Pune, 411007
India

Lymperopoulos Panagiotis
NMC Biolab
New Mexico Consortium
Los Alamos, New Mexico
USA

Manoj Prasad
National Institute of Plant Genome Research
New Delhi
India

Punita DL
Center for Biotechnology
Acharya Nagarjuna University
Guntur, 522510
India

Arnab Purohit
Department of Biotechnology
St. Xavier's College (Autonomous)
30, Mother Teresa Sarani
Kolkata, West Bengal
India

Roel Rabara
NMC Biolab
New Mexico Consortium
Los Alamos, New Mexico
USA

Rao KRSS
Center for Biotechnology
Acharya Nagarjuna University
Guntur, 522510
India

Sávio Pinho dos Reis
Universidade Federal do Pará
Belém, PA
Brazil

Aryadeep Roychoudhury
Department of Biotechnology
St. Xavier's College (Autonomous)
30, Mother Teresa Sarani
Kolkata, West Bengal
India

Anik Sarkar
Department of Botany
University of Calcutta
Kolkata, West Bengal
India

Sutanu Sarkar
Department of Genetics and Plant Breeding
Faculty of Agriculture
Bidhan Chandra Krishi Viswavidyalaya
Mohanpur, Nadia, West Bengal, 741252
India

Babar Shahzad
School of Land and Food
University of Tasmania
Hobart, Tasmania
Australia

Anket Sharma
Plant Stress Physiology Lab
Department of Botanical & Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

Savita Sharma
School of Biotechnology
Shri Mata Vaishno Devi University
Katra, J&K
India

Shelke DB
Department of Botany
Savitribai Phule Pune University
Pune, 411007
India

Gagan Preet Singh Sidhu
Department of Applied Sciences
UIET
Chandigarh, 160014
India

N. B. Singh
Department of Botany
University of Allahabad
Allahabad, Uttar Pradesh
India

Roshan Kumar Singh
National Institute of Plant Genome Research
New Delhi
India

Vivek K. Singh
School of Physics
Shri Mata Vaishno Devi University
Katra, J&K
India

Cláudia Regina Batista de Souza
Universidade Federal do Pará
Belém, PA
Brazil

P. Suprasanna
Nuclear Agriculture and Biotechnology Division
Bhabha Atomic Research Centre
Trombay, Mumbai, Maharashtra
India

Eraldo José Madureira Tavares
Empresa Brasileira de Pesquisa Agropecuária
Petrolina, PE
Brazil

Liliane Souza Conceição Tavares
Universidade Federal do Pará
Belém, PA
Brazil

Ashwani Kumar Thukral
Plant Stress Physiology Lab
Department of Botanical & Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

Anita Tripathi
International Centre for Genetic Engineering and Biotechnology
New Delhi
India

Durgesh Kumar Tripathi
Amity Institute of Organic Agriculture
Amity University, Uttar Pradesh
I 2 Block, 5th Floor, AUUP Campus
Sector-125
Noida, 201313, UP
India

Nidhi Verma
School of Life Sciences
Jawaharlal Nehru University
New Delhi, 110067
India

Sandeep Kumar Verma
Institute of Biological Science
SAGE University
Kailod Kartal, Indore
Madhya Pradesh, 452020
India

Poonam Yadav
Plant Stress Physiology Lab
Department of Botanical & Environmental Sciences
Guru Nanak Dev University
Amritsar, 143005
India

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Plant Tolerance to Environmental Stress: Translating Research from Lab to Land

P. Suprasanna[1,3] and S. B. Ghag[2]

[1] *Nuclear Agriculture and Biotechnology Division, Bhabha Atomic Research Centre, Trombay, 400 085 Mumbai, India*
[2] *Department of Biology, UM-DAE Centre for Excellence in Basic Sciences, Kalina campus, Santacruz (East), Mumbai 400 098, India*
[3] *Homi Bhabha National Institute, Mumbai, 400 095, India*

1.1 Introduction

Food security for a burgeoning human population in a sustainable ecosystem is an important goal. However, the threat from climate change and unpredictable environmental extremes (Abberton et al. 2016) to plant growth and productivity (Lobell and Gourdji 2012; Gray and Brady 2016; Tripathi et al. 2016a) is increasing. Climate change-driven effects, especially from erratic environmental fluctuations, can result in increased prevalence of abiotic stresses and, pests and pathogens in crop plants (Chakraborty and Newton 2011; Batley and Edwards 2016). Various abiotic stresses such as drought, salinity, temperature, and heavy metals have been shown to diminish average yields by more than 50% for major crops (Wang et al. 2003; Pereira 2016; Tripathi et al. 2016c).

Over the years, considerable information has become available on the stress-related genetic repertoire of genes, quantitative trait loci and molecular networks governing plant responses to drought, salinity, heat, and other abiotic stresses (Krasensky and Jonak 2012; Liu et al. 2018). This knowhow about genes and their regulation will enable improvements in stress tolerance in crops, in the face of the imminent threat of climate change, impacting crop genetic diversity and the productivity of staple food crops. Global temperature rises of 2–3 °C are predicted to push crops toward extinction and even wild species that have so far been considered valuable genetic resource may also be affected. This will have negative consequences locally as well as globally, because the key traits for adaptiveness to climate change and variability adaptation may be lost forever. It is hence desirable that additional genetic variability should be introduced through mutagenesis or other approaches. Over the past few decades, great success has been achieved through selection, breeding, hybridization, recombination, and mutation to broaden genetic variability for important traits conferring adaptation of many species to changing biotic, climatic, and environmental pressures.

Crop plants are susceptible to climate-driven abiotic (elevated CO_2, heat, drought, salinity, flooding) and biotic effects (Chapman et al. 2012). Several reviews have critically discussed the impact of climate change on various crop systems (Ahuja et al. 2010;

Molecular Plant Abiotic Stress: Biology and Biotechnology, First Edition.
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Yadav et al. 2011; Tripathi et al. 2016a). Abiotic stresses elicit a plethora of morphological, physiological, biochemical, and molecular alterations (Singh et al. 2015a,b; Tripathi et al. 2016b, 2017; Singh et al. 2017; Suprasanna et al. 2018). The impact of stress has been shown to induce modulated gene function of structural genes, regulatory genes, and other master regulators (Zhu 2016; Patel et al. 2018). Plant defenses are endowed with molecular components of stress signal perception, osmotic and ionic homeostasis, hormone signaling, reactive oxygen species (ROS) scavenging systems, metabolic pathways, etc. (Figure 1.1). There are specific responses that are osmotic, hormonal, ionic, signal transduction, and transcription factor based, and there

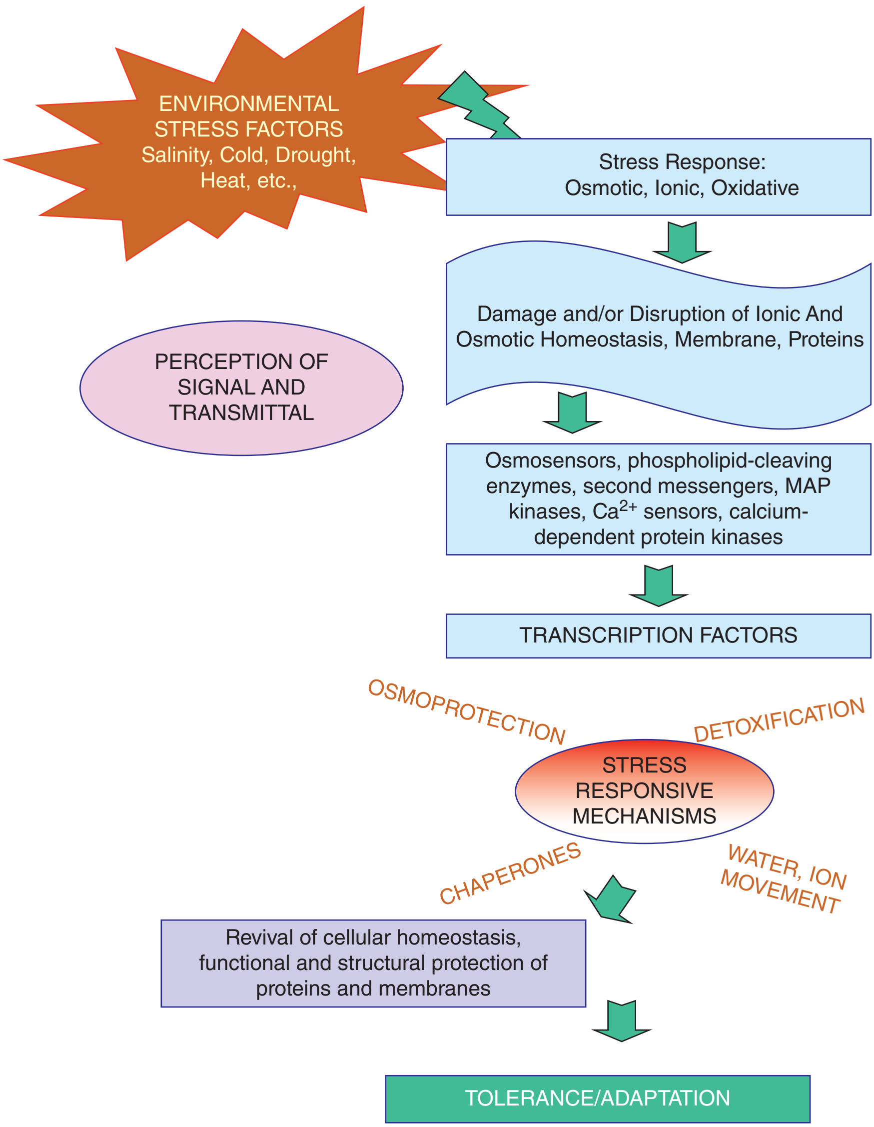

Figure 1.1 Abiotic stress impact and plant responses (Lokhande et al. 2012).

are also nonspecific responses that are activated by ROS (Mittler and Blumwald 2010, Muchate et al. 2016). Despite tremendous knowledge that has been generated in understanding abiotic stress responses, an integrated information gateway is needed to combine all of the genomics, proteomics, and metabolomics data concerning field conditions to achieve plant tolerance of environmental change (Roychoudhury et al. 2011, Edwards 2016). This has become a challenge that requires concerted effort. Hirayama and Shinozaki (2010) outlined some considerations (see Box 1.1) which should pave the way toward achieving this goal.

Box 1.1

- Sensor(s) and signaling pathways – perception and transduction of local stress signals under single and combined stresses.
- Molecular basis of interaction among biotic and abiotic stresses.
- Key factors in the crosstalk between abiotic stress responses and other plant developmental pathways.
- Long-term stress-associated responses under multiple abiotic stress conditions.
- Experimental conditions that simulate natural field conditions for testing and functional validation.

Modified after Hirayama and Shinozaki (2010).

Research into plant abiotic stress biology has two dimensions: the first, is the need to develop a detailed mechanistic view of plant responses to single and/or combined stresses to create a resource of gene targets and regulatory circuits for the improvement of stress-tolerant crop plants; and the second is the translation of research outcome into environmentally challenging field conditions. Physiological, biochemical, and molecular studies have generated data and great understanding of the mechanisms of how a plant will respond to a given stress or combined stress factors. Transcriptomic studies have demonstrated that the adaptation or responses are controlled by either up- or down-regulation of several genetic pathways and processes associated with stress perception and signaling (Munns and Tester 2008; Roychoudhury and Banerjee 2015). Transgenic approaches are available as the existing strategies for crop improvement programs based on biotechnology (Jewell et al. 2010). Genetic engineering for improved stress tolerance has been made possible through the manipulation of a single or a few effector genes or regulatory genes (Wang et al. 2016) or those that encode osmolytes, antioxidants, chaperones, water, and ion transporters (Chen et al. 2014; Paul and Roychoudhury 2018; Suprasanna et al. 2018). Various genes involved in the synthesis of osmoprotectants have been explored for their potential in improving abiotic stress tolerance (Reguera et al. 2012). In this article, we have reviewed the progress made in genetic engineering for abiotic stress tolerance, especially drought, salinity and cold, and highlight the potential areas for translational research in this field.

1.2 Drought Tolerance

Paucity of water is the most important environmental stress affecting crop plants, accounting for ~70% loss of potential yield worldwide (Shiferaw et al. 2014). Daryanto et al. (2016) investigated the data published from 1980 to 2015 that reported up to 21% and 40% yield reductions in wheat and maize, respectively, owing to drought worldwide. With changing climatic conditions and limited water supply, it is necessary to develop crop plants that can sustain drought conditions without reduced yield. Moreover, much lands are left barren due to poor water supply. Generating plants that can withstand drought stress will improve the food security for the growing population. Understanding of the physiological and biochemical basis of drought response and the gene regulatory networks relating to drought tolerance in plants is necessary. Remarkable studies have been carried out that identify the key regulators of drought response at different stages. These can be classified as: (i) drought induced transcriptional factors such as dehydration-responsive-element-bindings (DREBs), abscisic acid responsive element binding proteins (AREBs)/abscisic acid responsive element binding factors (ABFs), nuclear factor Y-B subunits (NF-YB), and tryptophan–arginine–lysine–tyrosine (WRKY) (Oh et al. 2005; Nelson et al. 2007; Xiao et al. 2009; Wu et al. 2009; Banerjee and Roychoudhury 2015); (ii) posttranscriptional and/or posttranslational modifications (Wang et al. 2008; Xiang et al. 2007; Kim et al. 2017); and (iii) production of osmoprotectant and molecular chaperones (Xiao et al. 2009; Bhaskara et al. 2015; Liu et al. 2015). Overexpressing or downregulating drought-responsive genes has yielded success in the laboratory. However, field studies demonstrating drought tolerance in plants are required to confirm the results.

Drought stress induces the synthesis or transportation of the phytohormone abscisic acid (ABA), which is a key molecule regulating signal events during drought impact (Fang and Xiong 2015). The initial perception of accumulation of ABA is through a complex of PYR (pyrabactin resistance)/PYL (PYR1-like)/RCARb (regulatory component of abscisic acid response), PP2C (protein phosphatase 2C), and SnRK2 (sucrose nonfermenting1-related protein kinase 2), which induces the expression of transcription factors NF-YA, SNAC (stress and abscisic acid-Inducible NAC), and AREBs (Roychoudhury and Paul 2012). These proteins further regulate the opening and closing of stomata to reduce transpirational water loss. Drought stress is also perceived by another regulatory loop through calcium-dependent protein kinase (CDPK) and calcineurin B-like protein-interacting protein kinase (CIPK), which activates AREB and DREBs that bind to the dehydration responsive element and abscisic acid responsive element *cis*-elements of downstream genes to produce the effector proteins such as late embryogenesis abundant protein (LEA), heat-shock protein (HSP), proline, glycine betaine, sugars, and polyamines (Yang et al. 2010). The overexpression of these transcription factors in drought-sensitive plants has improved tolerance of water-deficit conditions (Table 1.1). Moreover, some plants constitutively expressing drought-responsive transcription factors displayed growth retardation (Suo et al. 2012). To lessen this undesirable effect, researchers have employed stress-inducible promoters such as *HVA22P* to drive the expression of these transgenes in transgenic plants (Bhatnagar-Mathur et al. 2007; Xiao et al. 2009). However, when the drought stress is extended, it induces continuous expression of these genes in the transgenic plants, resulting in growth anomalies. To circumvent this problem, researchers have used stress-inducible tissue-specific promoters such as Responsive To Dehydration 29A (*RD29A*) for expressing these transgenes (Ito et al. 2006; Kasuga 2004). *RD29A* promoter is expressed only in the root tissues of rice plants under abiotic stress conditions. However, a small problem in root development could circumvent its use.

Table 1.1 List of genes used to generate drought-tolerant transgenic plants.

Target gene	Source of gene	Target plant	Evaluation	Functional change	References
AtABF3	*Arabidopsis thaliana*	*Oryza sativa* cv. Nakdong	Greenhouse	No visible growth abnormality, increased drought tolerance	Oh et al. 2005
SNAC1	Rice IRAT109	Rice (japonica)	Greenhouse, field	No growth anomaly, drought tolerance	Hu et al. 2006
OsNAC6	Rice cv. Nipponbare	Rice cv. Nipponbare	Greenhouse	Growth retardation, poor reproductive yields, increased tolerance to dehydration and enhanced resistance to blast disease	Nakashima et al. 2007
DREB1A	*Arabidopsis thaliana*	*Triticum aestivum*	Greenhouse	Delayed drought symptoms	Pellegrineschi et al. 2004
	Arabidopsis thaliana	*Arachis hypogaea* L. cv. JL 24	Greenhouse	40% higher transpiration efficiency than the untransformed controls	Bhatnagar-Mathur et al. 2007
OsDREB1G	*Oryza sativa* L. ssp. *japonica* cv. Zhonghua 11	*Oryza sativa* L. ssp. *japonica* cv. Zhonghua 11	Greenhouse	Improved tolerance to drought stress	Chen et al. 2008
OsDREB2B	*Oryza sativa* L. ssp. *japonica* cv. Zhonghua 11	*Oryza sativa* L. ssp. *japonica* cv. Zhonghua 11	Greenhouse	Improved tolerance to water deficit stress	Chen et al. 2008
OsDREB1F	*Oryza sativa*	*Oryza sativa* and *Arabidopsis*	Greenhouse	Enhanced tolerance to salt, drought, and low temperature	Wang et al. 2008
GhDREB	*Gossypium hirsutum*	*Triticum aestivum* L.	Greenhouse	Improved tolerance to drought, salt, and freezing stresses, increased accumulation of soluble sugar and chlorophyll in leaves under stress conditions	Gao et al. 2009
HhDREB2	*Halimodendron-halodendron*	*Arabidopsis*	Greenhouse	Increased tolerance to salt and drought stresses	Ma et al. 2015
GmDREB2	*Glycine max* L.	*Arabidopsis* and tobacco	Greenhouse	Enhanced tolerance to drought and high-salt stresses, high proline levels	
AtDREB2A-CA	*Arabidopsis thaliana*	*Gossypium hirsutum* L.	Greenhouse	Improved shoot development, improved morphometrics roots traits under water deficit	Lisei-de-Sá et al. 2017

(*continued*)

Table 1.1 (Continued)

Target gene	Source of gene	Target plant	Evaluation	Functional change	References
HARDY	*Arabidopsis*	O. *sativa* ssp. Japonica cv. Nipponbare	Greenhouse	Increased leaf biomass and bundle sheath cells, enhanced photosynthesis assimilation	Karaba et al. 2007
	Arabidopsis	*Trifolium alexandrinum* L.	Greenhouse, field	Thicker stems and more xylem rows per vascular bundle, resistant to lodging in the field, drought tolerance	Abogadallah et al. 2011
ZFP252	*Oryza sativa* L. cv. *Zhonghua 11*	*Oryza sativa* L. cv. *Zhonghua 11*	Greenhouse	Increased amount of free proline and soluble sugars, high-level expression of stress defense genes and enhanced rice tolerance to salt and drought stresses	Xu et al. 2008
ZFP182	*Oryza sativa* L. *subs. Japonica* cv. *Zhonghua 11*	*Oryza sativa* L. *subs. Japonica* cv. *Zhonghua 11*	Greenhouse	Increased accumulation of free proline and soluble sugars	Huang et al. 2012
DST	*Oryza sativa* L. cv. *Zhonghua 11*	*Oryza sativa* L. cv. *Zhonghua 11*	Greenhouse	Enhanced drought and salt tolerance in rice	Huang et al. 2009
ZAT10	*Arabidopsis thaliana*	*Oryza sativa* L. ssp. Japonica	Greenhouse, field	High spikelet fertility and high yield under drought stress	Xiao et al. 2009
NHX1	*Arabidopsis thaliana*	*Oryza sativa* L. ssp. Japonica	Greenhouse, field	High spikelet fertility and high yield under drought stress	Xiao et al. 2009
LOS5	*Arabidopsis thaliana*	*Oryza sativa* L. ssp. Japonica	Greenhouse, field	High spikelet fertility and high yield under drought stress	Xiao et al. 2009
	Arabidopsis thaliana	*Nicotiana tabacum*	Greenhouse	Higher water content, better cellular membrane integrity, accumulated higher quantities of ABA and proline, and higher levels of antioxidant enzymes	Yue et al. 2011
	Arabidopsis thaliana	Maize	Greenhouse	Reductions in stomatal aperture, higher relative water content and leaf water potential, lower leaf wilting, less electrolyte leakage, less malondialdehyde and H_2O_2 content, and higher levels of antioxidative enzymes and proline content	Lu et al. 2013

NPK1	*Arabidopsis thaliana*	*Oryza sativa* L. ssp. Japonica	Greenhouse, field	High spikelet fertility and high yield under drought stress	Xiao et al. 2009
LeNCED1	Tomato	*Petunia*	Greenhouse	Elevated leaf ABA concentrations, increased concentrations of proline, and increase in drought resistance.	Estrada-Melo et al. 2015
AtNF-YB1	*Arabidopsis thaliana*	*Arabidopsis thaliana*	Greenhouse	Higher water potential and photosynthesis rate	Nelson et al. 2007
ZmNF-YB2	*Zea mays*	Maize	Greenhouse, field	Increased chlorophyll content, stomatal conductance, leaf temperature, reduced wilting, and maintenance of photosynthesis under stress conditions	Nelson et al. 2007
TaNF-YB3	*Triticum aestivum*	Tobacco cv. Wisconsin 35	Greenhouse	Improved growth under drought, enhanced leaf water retention capacity, and increased antioxidant enzyme activities and osmolyte accumulation.	Yang et al. 2017
GmNFYB1	*Glycine max*	*Arabidopsis*	Greenhouse	Higher seed germination rate, longer root lengths, increased proline accumulation in leaves and decreased water loss under drought and salt stress conditions	Li et al. 2016
Cdt-NF-YC1	Bermuda grass *(Cynodon dactylon 9 Cynodon transvaalensis)*	*Oryza sativa* L. ssp. *japonica* cv. Zhonghua 11	Greenhouse	Increased tolerance to drought and salt stress and increased sensitivity to ABA	Chen et al. 2015a,b
OsWRKY11	*Oryza sativa* L.	*Oryza sativa* cv. Sasanishiki	Greenhouse	Slower leaf wilting and less impaired survival rate	Wu et al. 2009
PdNF-YB7	*Populus nigra* × *(Populus deltoides* × *Populus nigra)*	*Arabidopsis*	Greenhouse	Increased seed germination rate and root length and decrease in water loss, and displayed higher photosynthetic rate	Han et al. 2013

(*continued*)

Table 1.1 (Continued)

Target gene	Source of gene	Target plant	Evaluation	Functional change	References
DnWRKY11	*Dendrobium nobile*	*Nicotiana tabacum* cv. Huangmiaoyu	Greenhouse	Higher germination rate, longer root length, higher fresh weight, higher activities of antioxidant enzymes, and lower content of malonidialdehyde	Xu et al. 2014
FcWRKY70	*Fortunella crassifolia*	*Nicotiana nudicaulis* and *Citrus lemon*	Greenhouse	Higher expression levels of arginine decarboxylase and accumulated larger amount of putrescine	Gong et al. 2015
TaWRKY33	*T. aestivum* cv. Xiaobaimai	*Arabidopsis*	Greenhouse	Increased germination rates, promoted root growth and reduced water loss	He et al. 2016
FtbHLH3	*Fagopyrum tataricum*	*Arabidopsis*	Greenhouse	Lower malondialdehyde, ion leakage, and reactive oxygen species, higher proline content, activities of antioxidant enzymes, and increased photosynthetic efficiency	Yao et al. 2017
Musa DHN-1	*Musa* spp.	*Musa* spp.	Greenhouse	Improved tolerance to drought and salt-stress, increased accumulation of proline and reduced malondialdehyde levels	Shekhawat et al. 2011
AnnSp2	*Solanum pennellii*	*Solanum lycopersicum*	Greenhouse	Induced stomatal closure and reduced water loss, improved scavenging of ROS, higher total chlorophyll content, lower lipid peroxidation levels, increased peroxidase activities and higher levels of proline	Ijaz et al. 2017
SbPIP1	*Salicornia bigelovii*	*Nicotiana tabacum*	Greenhouse	Higher relative water content and proline content, but lower levels of malondialdehyde and less ion leakage	Sun et al. 2017a,b
DRIR	*Arabidopsis thaliana*	*Arabidopsis thaliana*	Greenhouse	Increased tolerance to drought and salt stress	Qin et al. 2017
Sly-miR169c	*Solanum lycopersicum*	*Solanum lycopersicum*	Greenhouse	Reduced stomatal opening and transpiration rate, lowered leaf water loss, and enhanced drought tolerance	Zhang et al. 2011
miR408	*Arabidopsis thaliana*	Chickpea	Greenhouse	Stunted growth, regulation of *DREB* genes	Hajyzadeh et al. 2015