Narendra Tuteja
Sarvajeet Singh Gill *Editors*

Plant Acclimation to Environmental Stress

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Professor E.A. Siddiq
(July 15, 1937 —)

Professor E.A. Siddiq was born in Ilayangudi, Tamil Nadu, India and received his B.Sc. from Madras University and his M.Sc. and Ph.D in Cytogenetics from Indian Agricultural Research Institute (IARI), New Delhi in 1958, 1964, and 1964, respectively. His main field of research is genetics, plant breeding, biotechnology, and his contributions in this field are significantly important. Professor Siddiq's research in the past three and half decades contributed significantly to the development of high *yielding dwarf basmati and non-basmati varieties and hybrid rice, thereby boosting rice production in India. His scientific work is featured in the most prestigious international journals. He is a member of various national and international societies, including the Board of Trustees, International Rice Research Institute (IRRI), the Philippines, and has published more than 200 research papers. Professor Siddiq is Adjunct Professor, University of Hyderabad, 2008 to date; Adjunct Faculty, Centre for DNA Fingerprinting and Diagnostics, Hyderabad, 2008 to date; Hon. Professor—Biotechnology, Acharya N.G. Ranga Agricultural University, Hyderabad, 2002 to date. Professor Siddiq received many Awards and Honors from various scientific bodies such as Hari Om Ashram Trust National Award, 1975; VASVIK Foundation National Award, 1981; Amrik Singh Cheema Award, 1987–1988; Om Prakash Bhasin Award, 1994; Rafi Ahmed Kidwai Prize, 1995; Norman Borlaug Award, 1995; INSA Silver Jubilee Medal, 1997; ISCA G.P. Chatterjee Memorial Lecture Award, 2001; Agriculture Leadership Award for Agricultural Research and Development, 2008; Padma shree, 2011; INSA Sundarlal Hora Medal, 2011; and NASI Senior Scientist Fellow, 2012.*

This book is dedicated to Professor E.A. Siddiq for nurturing plant genetics, plant breeding, and plant biotechnology.

Foreword

Agriculture is the base of food for all times. Thus, agricultural security is fundamental to the global food security. In agriculturally important countries, the sector is pivotal for generating economic growth and opportunity for overall livelihood security.

Towards the year 2050, the world population is projected to stabilize at around 9.2 billion. In order to adequately feed this population, the global agriculture must double its food production, and farm productivity would need to increase by 1.8 % each year—indeed a tall order. On the other hand, the natural resources—the agricultural production base, especially land, water, and biodiversity, are fast shrinking and degrading. For instance by 2025, 30 % of crop production will be at risk due to the declining water availability. Thus, in order to meet the ever-intensifying demand for food and primary production, more and more is to be produced from less and less of the finite natural and nonrenewable resource.

The bulk of the population increase will materialize in developing countries. Most of these are agriculture-dependent, and several of them are food deficit. Moreover, these countries have high concentration of smallholder resource-poor farmers and their agriculture is predominantly rainfed, which is inherently low-yielding and vulnerable to weather fluctuations.

The challenges of attaining sustainably accelerated and inclusive growth and comprehensive food security have been exacerbated by the global climate change and unusual fluctuations. The global warming due to rising concentration of greenhouse gases (GHGs) causing higher temperature, disturbed rainfall pattern causing frequent drought and flood, sea level rise, etc., is already adversely impacting productivity and stability of production, resulting in increased vulnerability, especially of resource-poor farmers. World Bank projects that the climate change will depress crop yields by 20 % or more by the year 2050. Recognizing that agriculture is both a victim of and a contributor to GHGs and other environmental pollutions, a two-pronged approach to reduce the emission and to develop adaptive measures to increase agricultural resilience will be needed.

Research and technology development (supported by policy and institutions) will need to be geared to meet the veritable challenges. We may recall, genetic alchemy of rice, wheat, and other major crops, which triggered the Green Revolution, is a shining example of science- and technology-led agricultural transformation immensely contributing to global food security and agrarian prosperity. With the greater emphasis on congruence of high productivity and sustainability in face of the intensifying volatilities due to climate change, biotic and abiotic stresses, and market instabilities, let alone the challenges of adequately feeding the swelling population from shrinking and degrading natural resources, new and modern sciences, and cutting-edge technologies, especially molecular breeding and genetic engineering for crop improvement and development of designer crops, will increasingly be called upon to provide the desired solutions.

This volume, *Plant Acclimatization to Environmental Stress*, ably compiled and edited by Drs. Narendra Tuteja and Sarvajeet Singh Gill, is a rich source of information on molecular, biochemical, microbial, and physiological bases of tolerance to abiotic stresses (drought, cold, salt, various toxicities, etc.) and on the development of tolerant varieties for adverse environmental conditions. It is hoped that researchers, scientists, and students, especially of crop biology, breeding, ecology, and production agronomy will greatly benefit from this volume. Most importantly, judicious use of this information should be used to develop crop varieties and management practices conducive to enhanced and resilient production leading to improved food, nutritional, ecological, and economic security.

I must congratulate the Editors and Springer for preparing this invaluable scientific resource.

New Delhi, India R.B. Singh

Preface

Abiotic stress factors mainly salinity, drought, flooding, and low and high temperature are the main elements which drastically limit the agricultural crop productivity globally. It has been estimated that salinity and drought are expected to cause serious salinization of more than 50 % of all available productive, arable lands by the year 2050. Extreme environmental events in the era of global climatic change further aggravate the problem and remarkably restrict the plant growth and development. Potential yield of economically important crops is drastically coming down every year just because of abiotic stresses. The mechanisms underlying endurance and adaptation to environmental stress factors have long been the focus of intense research. Plants overcome environmental stresses by the development of tolerance, resistance, or avoidance mechanisms. Plant acclimation to environmental stress is the process to adjust to a gradual change in its environment which allows the plants to maintain performance across a range of adverse environmental conditions.

In this book "Plant Acclimation to Environmental Stress," we present a collection of 17 chapters written by 50 experts in the field of crop improvement, genetic engineering, and abiotic stress tolerance. Plant Acclimation to Environmental Stress presents the latest ideas and trends on induced acclimation of plants to environmental stresses under changing environment. Various chapters included in this book provide a state-of-the-art account of the information is a resourceful guide suited for scholars and researchers working in the field of crop improvement, genetic engineering, and abiotic stress tolerance.

Chapter 1 deals with the use of priming agents towards plant acclimation to environmental stress. In this chapter, an up-to-date overview of the literature is presented in terms of some of the main priming agents commonly employed towards induced acclimation of plants to environmental challenges. Chapter 2 uncovers the sensing, signaling, and defending mechanisms in crop plants facing cold stress in the changing environment where authors discuss the status of effects of cold stress on plant metabolism, perception, and transduction of cold stress, genes expressed, defense mechanisms, and target genes for genetic engineering. Chapter 3 deals with drought and salinity tolerant biofuel crops for the Thar Desert. Chapter 4 covers strategies for the salt tolerance in bacteria and archeae and its implications in developing crops for adverse conditions. Chapter 5 deals with the adverse effects of abiotic stresses on medicinal and aromatic plants and their alleviation by calcium where authors emphasized that exogenously applied Ca can alleviate salt, heat, drought, high temperature, and cold stresses by regulation of antioxidant activities and discussed that in several plant cell-elicitor systems, the activation of defense responses depends on the presence of extracellular Ca. Thus, the growth, yield, and quality of the medicinal and aromatic plants could be improved under abiotic stress by supplying the plants with sufficient calcium nutrient. Chapter 6 discusses the role of DREB-like proteins in improving stress tolerance of transgenic crops. Chapter 7 focuses on Homeobox genes as potential candidates for crop improvement under abiotic stress. This chapter highlights the importance of homeobox genes in abiotic stress responses and their potential for engineering stress tolerance for crop improvement. Chapter 8 deals with APETALA2 gene family and its potential for crop improvement under adverse conditions. This chapter sheds light on transgenic expression of a single AP2 TF that has led to improved tolerance to multiple stresses like salinity, drought, and heat stress and pathogen infection, therefore emphasized that engineering of AP2 TFs seems to be a valuable tool towards achieving enhanced crop productivity under adverse conditions. Chapter 9 discusses the potential of osmoprotectants for crop improvement under adverse conditions. This chapter will encompass the potential role of osmoprotectants in plant stress adaptation and the possibilities for crop improvement. Chapter 10 deals with epigenetic modifications in plants under adverse conditions where authors discussed that epigenetic marks modify the properties of chromatin and change gene transcriptional states on the scale from the entire genome to a single specific gene. These marks allow for greater genome plasticity which results in better adaptation of plants to changing environmental conditions. Chapter 11 sheds light on the physiological role of nitric oxide in plants grown under adverse environmental conditions where authors reviewed recent progress in NO research in a broader context of abiotic stress tolerance and discussed its diverse roles in physiological and biochemical processes in plants and the protective mechanisms it exhibits towards abiotic stress tolerance. Chapter 12 deals with weeds, as a source of genetic material for crop improvement under adverse conditions. In this chapter an effort has been made to point out the useful traits of the weeds which can be transferred into crop plants for improvement along with the few successful case studies. Chapter 13 talks about sustainable agriculture practices for food and nutritional security and authors discussed the issues related to sustainability of existing agriculture; lessons learnt from green revolution; and possibility of new technologies so as to have sustainable ever green revolution. Chapter 14 deals with approaches for abiotic stress tolerance in crop plants for sustainable agriculture by the use of arbuscular mycorrhiza. Chapter 15 deals with the potential use of biofertilizers as a sustainable eco-friendly agricultural approach to crop improvement. Chapter 16 deals with plant–pathogen interactions and crop improvement under adverse conditions. Chapter 17 uncovers whether G-proteins may be the key elements for overcoming environmental stresses and increasing crop yield in plants? In this chapter the authors discuss the stress in general followed by the role of GPCR and G-proteins in biological processes including those that are related to environmental stresses.

The editors and contributing authors hope that this book will include a practical update on our knowledge for plant acclimation to environmental stress and lead to new discussions and efforts to the use of various tools for the improvement of crops for abiotic stress tolerance.

We are highly thankful to Dr. Ritu Gill, Centre for Biotechnology, MD University, Rohtak for her valuable help in formatting and incorporating editorial changes in the manuscripts. We would like to thank Professor R.B. Singh, President, National Academy of Agricultural Sciences, New Delhi for writing the foreword and Springer Science+Business Media, New York, particularly Daniel Dominguez, Developmental Editor/Project Manager; Andy Kwan, Assistant Editor, and Eric Stannard, Editor, Botany for their professional support and efforts in the layout. This book is dedicated to Professor E.A. Siddiq for nurturing plant genetics, plant breeding, and plant biotechnology.

New Delhi, India Narendra Tuteja
Rohtak, India Sarvajeet Singh Gill

Editors

Narendra Tuteja

Narendra Tuteja was born in 1955. Currently, Dr. Tuteja is working as Group Leader and Senior Scientist in Plant Molecular Biology Group, International Centre for Genetic Engineering and Biotechnology (ICGEB), New Delhi. Dr. Tuteja obtained his M.Sc., Ph.D., and D.Sc. in Biochemistry from the Lucknow University in 1977, 1982, and 2008, respectively. He is fellow of the Academies of Sciences: FNASc. (2003), FNA (2007), FASc. (2009), FNESA (2009), and FTWAS (2011).

Dr. Tuteja has made major contributions in the field of plant DNA replication and abiotic stress signal transduction, especially in isolating novel DNA/RNA helicases and several components of calcium and G-proteins signaling pathways. Initially he made pioneer contributions in isolation and characterization of large number of helicases from human cells while he was at ICGEB Trieste and published several papers in high impact journals including *EMBO J.* and *Nucleic Acids Res.* From India he has cloned the first plant helicase (*Plant J.* 2000) and presented the first direct evidence for a novel role of a pea DNA helicase (*Proc Natl Acad Sci U S A*. 2005) in salinity stress tolerance, pea heterotrimeric G-proteins (*Plant J*. 2007) in salinity, and heat stress tolerance. Dr. Tuteja has reported the first direct evidence in plant that PLC functions as an effector for Gα subunit of G-proteins. All the above work has received extensive coverage in many journals, including Nature Biotechnology, and bulletins all over the world. His group has also discovered novel substrate (pea CBL) for pea CIPK (*FEBS J*. 2006). He has already developed the salinity-tolerant tobacco and rice plants without affecting yield. Recently, few new high salinity stress-tolerant genes (e.g., Lectin receptor-like kinase, Chlorophyll a/b-binding protein, and Ribosomal L30E) have been isolated from *Pisum sativum* and have been shown to confer high salinity stress tolerance in bacteria and plant (*Glycoconjugate J*. 2010; *Plant Signal. Behav*. 2010). Recently, very high salinity stress-tolerant genes from fungus *Piriformospora indica* have been isolated and their functional validation in fungus and plants is in progress. Overall, Dr. Tuteja's research uncovers three new pathways to plant abiotic stress tolerance. His results are an important success and indicate the potential for improving crop production at suboptimal conditions.

Sarvajeet Singh Gill

Sarvajeet Singh Gill was born on January 21, 1979. Dr. Gill obtained his B.Sc. (1998) from Y.D. College, Kanpur University and M.Sc. (2001, Gold Medalist), M.Phil. (2003), and Ph.D (2009) from Aligarh Muslim University. Presently, Dr. Gill is working as Assistant Professor in Centre for Biotechnology, MD University, Rohtak, Haryana.

Dr. Gill's main area of research includes Genetic Engineering, Stress Physiology, and Molecular Biology (Development of abiotic stress-tolerant crop plants, the physiological, biochemical, and molecular characterization of agronomically important plants under abiotic stress factors, involvement of mineral nutrients, and other biotechnological approaches in the amelioration of abiotic stress effects in crop plants, use of a combination of genetic, biochemical, genomic, and proteomic approaches to understand the responses of various components of antioxidant machinery to abiotic stress and stress signaling, and stress tolerance in crop plants. Dr. Gill has several research papers, review articles, and book chapters to his credit in the journals of national and international repute and in edited books. He has edited four books namely *Sulfur Assimilation and Abiotic Stress in Plants*; *Eutrophication: Causes, Consequences and Control*; *Plant Responses to Abiotic Stress, Omics and Abiotic Stress Tolerance*; and *Improving Crop Resistance to Abiotic Stress*, published by Springer-Verlag (Germany), IK International, New Delhi, Bentham Science Publishers and Wiley-VCH, Verlag GmbH & Co. Weinheim, Germany, respectively. Dr. Gill is a regular reviewer of National and International journals and grants. He was awarded Junior Scientist of the year award by National Environmental Science Academy New Delhi in 2008. With Dr. Tuteja, Dr. Gill is working on heterotrimeric G-proteins Minichromosome maintenance (MCM) proteins and plant DNA helicases to uncover the abiotic stress tolerance mechanism in rice. The transgenic plants overexpressing heterotrimeric G-proteins and plant DNA helicases may be important for improving crop production at suboptimal conditions.

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Chapter 1
Plant Acclimation to Environmental Stress Using Priming Agents

Panagiota Filippou, Georgia Tanou, Athanassios Molassiotis, and Vasileios Fotopoulos

1 Introduction

Several reports have provided increasing evidence that plants can be "conditioned" for more rapid or intense induction of defense responses leading to enhanced resistance to biotic and abiotic stresses (Beckers and Conrath 2007). An analogy therefore exists with the concept of vaccination in animals, where the administration of antigenic material results in the stimulation of adaptive immunity to a disease and the ultimate prevention or amelioration of the effects of infection by pathogens. The physiological state in which plants are able to activate defense responses faster, better, or both, is called the primed state of the plant. Priming may be initiated in response to an environmental cue that reliably indicates an increased probability of encountering a specific stress factor, but a primed state may also persist as a residual effect following an initial exposure to the stress. The primed state can also be induced upon treatment with an acclimation-inducing agent, such as natural or synthetic compounds, as well as by colonization of plant tissues with beneficial microorganisms such as bacteria and arbuscular-mycorrhizal (AM) fungi. Under conditions of stress pressure, primed plants exhibit a higher fitness than non-primed plants or defense-expressing plants. Although priming has been known to occur in plants for several decades, most progress in the understanding of this phenomenon has been made over the past few years. The present chapter represents an up-to-date overview of the literature in terms of some of the main priming agents commonly employed toward induced acclimation of plants to environmental challenges. These include nitric oxide (NO),

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hydrogen peroxide (H_2O_2), hydrogen sulfide (H_2S), polyamines and beneficial microorganisms. However, it should be pointed out that several more priming agents exist and are successfully employed toward induced acclimation of plants to environmental stress, including the quaternary amine glycine betaine and β-aminobutyric acid. Some of the key research carried out with the use of the specific priming agents under examination are summarized in Table 1.1.

2 Nitric Oxide

Nitric oxide (NO) is a redox-reactive, small, diffusible, ubiquitous, bioactive gaseous molecule that participates in a multitude of physiological and developmental processes in plants, including the response to environmental stimuli. For instance, heat, salt, and hyperosmotic stress induce NO production in tobacco (*Nicotiana tabacum*) cell suspensions (Gould et al. 2003). Also, NO metabolism is modulated during different abiotic stress conditions (high light intensity, low and high temperature, continuous light, continuous dark, and mechanical wounding) in pea plants (Corpas et al. 2008). It is well established that the endogenous NO can have two opposite physiological roles: a high cellular production of NO can provoke extensive cellular damage whereas NO at low levels participates in various signaling pathways (del Rio et al. 2004; Lamattina et al. 2003). However, many questions remain concerning exactly how NO is produced and scavenged, and how this signal is perceived and propagated in defined biological responses in stressed plant cells (Gupta et al. 2011).

Even though the details remain to be resolved, an increasing number of articles have been published during the last decade concerning the effects of exogenous NO on alleviating abiotic stress in plants (reviewed in Baudouin 2011; Besson-Bard et al. 2008). It has also been increasingly evident that prior exposure to NO renders plants more resistant to future environmental stress, thereby suggesting that NO acts as a priming agent (reviewed in Molassiotis et al. 2010). In pioneering reports, Uchida et al. (2002) showed that pre-exposure of rice seedlings to sodium nitroprusside (SNP; a NO donor) resulted in protection against salt and heat stress, preventing the impairment of photosystem II, activating the enzymatic antioxidant machinery, and increasing the transcriptional levels of genes encoding sucrose-phosphate synthase, D-pyrroline-5-carboxylate synthase, and small heat shock protein 26. The priming function of pretreatments with NO against salinity stress was also confirmed in other plant species, including maize (Zhang et al. 2004), *Arabidopsis* (Wang et al. 2009; Zhao et al. 2007), cucumber (Fan et al. 2007), citrus (Tanou et al. 2009a, b), and also in germinating seeds in saline environment (Kopyra and Gwóźdź 2003; Li et al. 2005). In experiments performed with callus cell cultures under salt conditions, it was found that NO could regulate plasma membrane H^+-ATPase activity, thus increasing K^+/Na^+ ratio leading to salt acclimation (Wang et al. 2009; Zhao et al. 2004). The hypothesis that NO-mediated regulation of Na^+ homeostasis and K^+ acquisition via ATPase is an important salt acclimation mechanism in plants was also supported in *Arabidopsis* plants (Zhao et al. 2007). Other NO-driven cellular

Table 1.1 Selected priming agents (compounds or beneficial organisms) inducing tolerance to abiotic stress factors in the greenhouse and field

Priming agent	Abiotic Stress	Plant	Reference(s)
Nitric oxide	Salt	Rice	Uchida et al. (2002)
		Maize	Zhang et al. (2004)
		Arabidopsis	Zhao et al. (2007), Wang et al. (2009))
		Cucumber	Fan et al. (2007)
		Citrus	Tanou et al. (2009a, b, 2010)
	Heat	Rice	Uchida et al. (2002)
		Reed	Song et al. (2008)
		Arabidopsis	Lee et al. (2008)
	Cold	Cucumber	Cui et al. (2011)
		Loquat	Wu et al. (2009)
		Arabidopsis	Zhao et al. (2009); Cantrel et al. (2011)
	Drought	Wheat	Garcia-Mata and Lamattina (2001)
		Rice	Farooq et al. (2009)
	UV-B radiation	Maize	An et al. (2005); Wang et al. (2006)
		Bean	Shi et al. (2005)
		Arabidopsis	Zhang et al. (2009d)
	Heavy metals	Rice	Singh et al. (2009); Xiong et al. (2009)
		Tomato	Wang et al. (2010b)
		Tobacco	Ma et al. (2010)
		Yellow lupin	Kopyra and Gwóźdź (2003)
		Arabidopsis	Graziano and Lamattina (2005)
Hydrogen peroxide	Cold	Maize	Prasad et al. (1994)
		Bean	Yu et al. (2003)
		Sweet potato	Lin and Block (2010)
		Mustard	Kumar et al. (2010)
	Salt	Rice	Uchida et al. (2002)
		Wheat	Wahid et al. (2007); Li et al. (2011)
		Citrus	Tanou et al. (2009a, b, 2010)
		Maize	Neto et al. (2005)
		Oat	Xu et al. (2008)
		Barley	Fedina et al. (2009)
		Pigeonpea	Chawla et al. (2010)
	Heat	Rice	Uchida et al. (2002)
		Bentgrass	Larkindale and Huang (2004)
		Cucumber	Gao et al. (2010)
	Heavy metals	Pigeonpea	Chawla et al. (2010)
		Wheat	Xu et al. (2011)
		Rice	Chao and Kao (2010)
Hydrogen sulfide	Salt	Strawberry	Christou, Fotopoulos et al. (unpublished data)
		Wheat	Zhang et al. (2010a)
		Sweet potato	Zhang et al. (2009c)
	Drought	Wheat	Shan et al. (2011)
		Arabidopsis	Garcia-Mata and Lamattina (2010)
		Broad bean	Garcia-Mata and Lamattina (2010)
		Soybean	Zhang et al. (2010b)
	Heavy metals	Cucumber	Wang et al. (2010a)
		Wheat	Zhang et al. (2008a, 2010a, c)
	Cold	Wheat	Stuiver et al. (1992)

(continued)

Table 1.1 (continued)

Priming agent	Abiotic Stress	Plant	Reference(s)
Polyamines	Salt	Oat	Besford et al. (1993)
		Rice	Maiale et al. (2004); Ndayiragije and Lutts (2006a, b, 2007); Quinet et al. (2010)
		Mustard	Verma and Mishra (2005)
		Spinach	Öztürk and Demir (2003)
		Arabidopsis	Kusano et al. (2007)
	Drought	Rice	Yang et al. (2007)
		Arabidopsis	Kusano et al. (2007)
Beneficial microorganisms	Heavy metals	*Arabidopsis*	Farinati et al. (2011)
	Cold	Blue mustard	Ding et al. (2011)
		Grapevine	Ait-Barka et al. (2006)
	Salt	Maize	Harman (2006); Abdelkader and Esawy (2011)
		Poplar	Luo et al. (2009)
		Tomato	Latef and He (2011)
		Olive	Porras-Soriano et al. (2009)
	Drought	Rice	Ruiz-Sánchez et al. (2010)
		Soybean	Porcel and Ruiz-Lozano (2004)
		Citrus	Fan and Liu (2011)
		Southern Beech	Alvarez et al. (2009)

responses toward salt stress acclimation involve the increase in chlorophyll content, the decrease in electrolyte leakage along with changes in polyamine metabolism (Zhang et al. 2004), the increase in the activities of endopeptidase and carboxypeptidase (Zheng et al. 2010), and the induction of ATP synthesis and the respiratory electron transport in mitochondria (Yamasaki et al. 2001; Zottini et al. 2002). In addition, Tanou et al. (2009b) provided evidence that NO exhibits a strong antioxidant role during the establishment acclimation of citrus plants to salinity. More interestingly, a proteomic study on citrus plants grown under salinity stress by Tanou et al. (2009a) provided a wide list of proteins whose accumulation levels are regulated by salt stress, whereas it was further shown that exogenous supply of NO via root pretreatment with SNP reversed a large part of the NaCl-responsive proteins. These SNP/NaCl-responsive proteins are mainly involved in photosynthesis, defense mechanism, and energy/glycolysis pathways. These data indicate that NO pre-exposure can specifically modify protein expression signatures, and that a NO-specific priming function is needed for a proper salt acclimation response.

In addition to NO-mediated priming phenomena against salinity stress, several studies demonstrated that NO is also involved in drought acclimation in many plant species, including wheat (Garcia-Mata and Lamattina 2001), reed cell suspension cultures (Zhao et al. 2008), and rice (Farooq et al. 2009). These results were followed by findings indicating the involvement of NO in the maintenance of tissue water potential through stomatal closure (Garcia-Mata et al. 2003), alleviation of oxidative damage via protein synthesis acceleration, photosynthesis rate enhancement, and stimulation of antioxidant enzymes activities (Tan et al. 2008). Apart from an osmotic stress alleviation inducing molecule, there is also evidence that NO is also an osmotic stress induced molecule in a biphasic manner through an early production phase followed by a lateral one (Kolbert et al. 2007). Notably, NO was previously shown to be involved in the ABA-induced stomatal closure (Bright et al. 2006) via activating mitogen-activated protein kinase (MAPK) (Zhang et al. 2007). In this sense, transgenic tobacco plants over expressing *SgNCED1* gene encoding the 9-*cis*-epoxy-carotenoid dioxygenase, which accounts for increased ABA biosynthesis, resulted in a NO-associated drought and salt stress acclimation (Zhang et al. 2009a).

Within the context of temperature stress, NO is also known to be involved in the plant response to high- and low-temperature stresses. There is evidence that NO exhibits priming phenomena under heat stress conditions (Uchida et al. 2002), but in an ABA-independent manner (Song et al. 2008). Ion leakage prevention, growth and cell viability retention, decreased H_2O_2 and MDA contents, and increase in antioxidant enzyme activities have been reported to be responses to heat acclimation via NO pretreatment (Song et al. 2008). In a study conducted with transgenic *Arabidopsis* plants impaired in NO synthesis, this was directly connected with lack of thermotolerance (Xuan et al. 2010) since the transgenic plant cannot accumulate a specific heat shock protein (Hsp18.2). However, the NO-induced priming against heat stress seems to be more a complicated scenario. For example, Lee et al. (Lee et al. 2008) showed that *S*-nitrosoglutathione reductase (GSNOR), the enzyme which metabolizes the NO adduct *S*-nitrosoglutathione, is necessary for the acclimation of *Arabidopsis* plants to high temperature. These authors also found that *Arabidopsis* mutants lacking HOT5 (encoding GSNOR) were thermosensitive but NO donors failed to rescue thermotolerance (Lee et al. 2008). Clearly, these observations need to be developed further to establish the specific roles of Hsp and especially of GSNOR in cold acclimation and, most importantly, their interplay with NO during this process. On the other hand, NO priming action against cold stress seems to be mediated by brassinosteroids (BRs). Indeed, pretreatment of cucumber plants with NO donors leads to cold acclimation and to the induction of antioxidant enzymes (Cui et al. 2011). Pharmacological studies with Arabidopsis plants using nitric reductase (NR) inhibitor, NO scavenger, and NO donor showed that NR-dependent NO production was linked with freezing acclimation via increasing the expression levels of *P5CS1* and *ProDH* genes and enhanced accumulation of proline (Zhao et al. 2009). Another report supports that NO-induced cold acclimation is associated with scavenging ability of NO against ROS (Wu et al. 2009), whereas a more recent study on *Arabidopsis* revealed that genetic impairment of NO accumulation upon chilling inhibited the expression of specific cold-responsive genes, phosphatidic acid synthesis, and sphingolipid phosphorylation (Cantrel et al. 2011).

Another severe abiotic damaging factor on plant metabolism is UV-B radiation (250–320 nm), resulting in disturbances in plant growth and development (Rozema et al. 1997). Early studies revealed that plants undergoing UV-B exposure produce NO leading also in the expression of UV-B radiation-specific defense genes

(Mackerness et al. 2001). The protective signaling effects of NO against UV-B treatment were previously established in maize seedling receiving NO hydroponically (via SNP application) (An et al. 2005), in bean leaves sprayed with SNP (Shi et al. 2005) or in SNP-treated *Cyanobacterium* cell suspension cultures (Xue et al. 2007). According to Shi et al. (2005), NO could partially alleviate the decrease in chlorophyll content and F_v/F_m ratio caused by UV-B exposure, probably by mediating the activities of antioxidant enzymes. Xue et al. (2007) suggested also the participation of reduced glutathione (GSH) in the NO-mediated acclimation against UV-B exposure. In addition, Wang et al. (2006) proposed that NO acts in the same direction or synergistically with ROS to induce ethylene biosynthesis in the leaves of maize seedlings under UV-B radiation; however, the connection of this crosstalk with acclimation against UV-B irradiation has not been established yet. Meanwhile, Zhang et al. (2009d), using AtNOS1 mutant Arabidopsis plants impaired in regular NO biosynthesis and containing lower amount of NO, showed that these plants were prone to UV-B damage, whereas NO supplementation could alleviate the oxidative damaged by increasing flavonoid and anthocyanin contents.

Recently, the alleviating effects of exogenous NO on heavy metal toxicity in plants are becoming apparent (reviewed in Hasanuzzaman et al. 2010; Xiong et al. 2010), including arsenic toxicity in roots of *Oryza sativa* (Singh et al. 2009), copper toxicity in tomato plants (Wang et al. 2010b), cadmium toxicity in tobacco (Ma et al. 2010), and zinc toxicity in *Solanum nigrum* (Xu et al. 2010). In addition, there is evidence that NO is involved in the acclimation of various cell systems against multiple heavy metals stress (Kopyra and Gwóźdź 2003). By contrast to these observations, Arasimowicz-Jelonek et al. (2011) found that NO contributes to Cd toxicity by promoting Cd uptake and participates in metal-induced reduction of root growth. In several studies conducted with various plant species exposed to single (Singh et al. 2009; Wang et al. 2010b) or combined multiple heavy metal stressors (Kopyra and Gwóźdź 2003), it was evidenced that exogenous application of NO resulted in the modulation of the antioxidant mechanism or in the scavenging of ROS. In addition, Xiong et al. (2009) demonstrated that NO-induced acclimation to Cd toxicity in rice is attributed to the decreased distribution of Cd in the soluble fraction of leaves and roots and in the increased distribution of Cd in the cell walls of roots. Furthermore, a NO-driven reduced transpiration rate with concomitant decreased heavy metal translocation from roots to shoots has also been proposed, but without further cross-verification of the effect of exogenously applied SNP to stomatal movement (Xiong et al. 2009). Another interesting mechanism through which NO could act as a signaling factor under heavy metal toxicity situations is its action as a regulator of stress-related genes. For example, the regulation of iron homeostasis by ferritin gene expression in Arabidopsis leaves has been proven to be attributed to exogenous NO application (Graziano and Lamattina 2005) whereas NO production in algae under Cu toxicity has been shown to be implicated in up-regulation of the expression of *P5CS* which encodes D1-pyrroline-5-carboxylate synthetase responsible for proline biosynthesis (Zhang et al. 2008b).

3 Hydrogen Peroxide

It is now well established that virtually all biotic and abiotic stresses induce or involve oxidative stress to some degree, and the ability of plants to control oxidant levels is highly correlated with stress acclimation (Gill and Tuteja 2010a). Hydrogen peroxide (H_2O_2) is usually the end step conversion of ROS, which, despite its reactive perception is the most stable molecule among them (Hung et al. 2005). In addition to being toxic and causing cell death at high concentrations (Dat et al. 2000), H_2O_2 has been regarded as a central player in growth and developmental processes of plants (Hung et al. 2005). Currently, H_2O_2 is considered to be a messenger molecule to various abiotic and biotic stress conditions when applied at low concentrations and a number of acclimation mechanisms based on the physiological and biochemical changes inquired have been proposed (Fukao and Bailey-Serres 2004; Mittler et al. 2004). These mechanisms normally include genes encoding antioxidants, cell rescue/defense proteins, and signaling proteins such as kinase, phosphatase, and transcription factors (Hung et al. 2005).

One of the first studies regarding chilling stress acclimation reported that chilling imposed oxidative stress in maize seedlings could be prevented by H_2O_2 pretreatment by increasing *cat3* transcripts and the enzymatic activities of catalase3 and guaiacol peroxidase (Prasad et al. 1994). In this report, the dual role of H_2O_2 at low temperatures was proposed, since H_2O_2 early accumulation triggered the production of antioxidant enzymes whereas H_2O_2 accumulated to damaging levels in the tissues at non-pretreated and therefore non-acclimated seedlings (Prasad et al. 1994). A H_2O_2-induced chilling acclimation mechanism was also reported in mung bean plants via the induction of GSH (Yu et al. 2003). In studies with sweet potato (*Ipomoea batatas*) and sweet peppers (*Capsicum annuum*), it was evidenced that exogenously applied H_2O_2 may lead to chilling acclimation; however, the practical benefits of exogenous H_2O_2 application could not be clearly observed under all experimental conditions tested (Lin and Block 2010). In addition, it was observed that H_2O_2 pretreatment had beneficial effects in sweet potato against chilling injury when the pretreatment was applied under long photoperiod whereas this was not the case when it was applied under short photoperiod. These observations revealed that the H_2O_2-mediated priming phenomena may also be regulated by other intra- or extracellular factors. Brassinosteroids (BRs), such as 24-epibrassinolide, have been proposed to be involved in the H_2O_2-induced acclimation against chilling stress in *B. juncea* L. seeds and seedlings (Kumar et al. 2010). In this study it was supported that 24-epibrassinolide helped in alleviating the toxic effect of H_2O_2 through modulation of the antioxidant enzymes such as catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (SOD) (Kumar et al. 2010). Comparable results to those were shown in a study with tomato plants, where BRs applied exogenously could alleviate drought-induced oxidative stress via increase in the activity of antioxidant enzymes and antioxidant compounds such as ascorbate, carotenoids, and proline (Behnamnia et al. 2009). The regulation of the enzymatic antioxidant machinery under heat stress conditions by H_2O_2 pretreatment and a resulting reduction of the oxidative