



Metabolic Adaptations in Plants During Abiotic Stress

Akula Ramakrishna
Sarvajeet Singh Gill

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Edited by
Akula Ramakrishna and Sarvajeet Singh Gill



CRC Press

Taylor & Francis Group

Boca Raton London New York

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CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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Printed on acid-free paper

International Standard Book Number-13: 978-1-138-05638-1 (Hardback)

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Library of Congress Cataloging-in-Publication Data

Names: Ramakrishna, Akula, editor. | Gill, Sarvajeet Singh, editor.
Title: Metabolic adaptations in plants during abiotic stress / editor(s):
Akula Ramakrishna and Sarvajeet Singh Gill.
Description: Boca Raton, FL : CRC Press, Taylor & Francis Group, 2018.
Identifiers: LCCN 2018016983 | ISBN 9781138056381 (hardback : alk. paper)
Subjects: LCSH: Plants--Metabolism. | Plants--Effect of stress on. |
Plants--Adaptation.
Classification: LCC QK881 .M43 2018 | DDC 581.7--dc23
LC record available at <https://lccn.loc.gov/2018016983>

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Dr. Ravishankar Gokare

This book is dedicated to Dr. Ravishankar Gokare, a renowned plant biotechnologist

and food biotechnologist of international repute.

Ravishankar Gokare was born in 1954 in Bangalore. He completed his BSc in 1972 at Bangalore University and further studies, MSc and PhD, in botany at the M.S. University of Baroda. He was a PhD student of Professor Atul R. Mehta, a renowned plant tissue culturist trained in the lab of Professor H.E. Street at Swansea, who was known as the Father of Modern Plant Tissue Culture. During his PhD he worked on metabolic regulation of secondary pathways in plants. He continued his postdoctoral work at CSIR Laboratory at Jammu-Tawi working on medicinal plants. He joined the Central Food Technological Research Institute, Mysore, in 1984 as Scientist B, where he had the fortune of working with India's most vibrant Algal Research Group, which was started by Dr. Wolfgang Becker of University of Tübingen in association with the eminent algal biotechnologist, Dr. L.V. Venkataraman. He rose to the level of Chief Scientist and Head of Plant Cell Biotechnology Department, a position he held for over 18 years.

Ravishankar initiated plant biotechnology and food biotechnology research at the Central Food Technological Research Institute (CFTRI), where he established a strong research group working on aspects of micro-propagation, conservation of biodiversity, bioactive metabolites, biosynthetic pathways in plants and microbes, metabolic regulation of secondary metabolites, post-harvest technologies for value addition to foods, and downstream processing of metabolites of food applications, such as food pigments, non-nutritive sweeteners, flavor molecules, etc. He was a pioneer in using elicitor technology to enhance metabolite yield in a standing crop of various plantation crops, which followed as an agronomic practice in various countries. Ravishankar is a plant conservation expert responsible for developing the tissue culture technology for a banana variety, Nanjangud Rasabale, which was facing the brink of extinction. Similarly, he was responsible for the development of technology for *Decalepis hamiltonii* (swallow root), a rich herb for adding value as a potent antioxidant source and an anticancer agent with the development of several recipes for health food application, including health drinks. The technology of swallow root was combined with the development of a mass production system through tissue culture methodology and the agronomic practice of cultivation, allowing for the conservation and sustainable utilization of this endangered herb. The benefits of this technology were transferred to the Soliga Tribes of BR Hills who are custodians of the germplasm, exemplifying the sharing of Intellectual Property Rights. Under Ravishankar's leadership, this was acclaimed as a star project of the Department of Science and Technology of the Government of India. In 1992, he received the Indian Science Congress Award for Young Scientist from the then Prime Minister of India for these contributions.

Ravishankar moved from metabolic regulation of secondary pathways to metabolic engineering in several systems. His group pioneered in the initiation of coffee biotechnology research under the Jai Vigyan project of the Government of India, sponsored by the Department of Biotechnology, which resulted in the development of transgenic coffee plants with lowered caffeine. The technology is useful for improvement of coffee plants for various traits. Various institutions including the Coffee Board, which collaborated under the All India Coordinated Project, benefited from the transformation system developed by his group. Ravishankar and his team

worked on metabolic engineering of carotenoids in algae, with the production of astaxanthin in *Dunaliella* spp., which is otherwise known for β -carotene only. This was achieved by cloning the genes of astaxanthin pathway from *Haematococcus pluvialis* into *Dunaliella*. Similarly, the metabolic engineering of fatty acid production to produce gamma linolenic acid in soybean by the expression of the Delta 6 desaturase gene of *Spirulina* is another example of his innovative research. He is also well known for his studies on genomics in higher plants and microalgal systems. These studies earned him a coveted award in new biology given by the Indian Science Congress Association.

Ravishankar is known for his contributions with Dr. L.V. Venkatraman in commercializing spirulina technology in India. This is a model for several other biotechnologists in India wherein the involvement of industry was realized from the beginning of the scale-up to the transfer of technology, culminating in Asia's largest spirulina production unit in Nanjangud by Bhallarpur Industries Limited. This contribution was recognized by the Government of India with a National Technology Day Award in 2003. Presently, the Government of Karnataka has taken up spirulina supplementation for malnourished children, under the mid-day meal program. His group have developed several value-added spirulina food products for meeting the micronutrient deficiencies caused by a deficiency of iron, gamma linolenic acid, and vitamin A in staple diets. Ravishankar is a great mentor, too. He has guided over 25 PhD students as a supervisor and mentored over 160 graduate students, who have occupied high positions in India and abroad in academia, R&D labs, and in industry. He has been a popular teacher who is known for motivating young minds. His love for the academics and student-centric activities have been well recognized at his present role as Vice President of Life Sciences and Biotechnology at Bangalore's pioneering research and innovation driven institution, namely Dayananda Sagar Institutions/Dayananda Sagar University at Bengaluru.

His innovative ideas, hard work, and dedication is evidenced by the publication of 340 research and review papers in peer-reviewed journals and over 45 patents awarded in India and abroad. His work has received over 13,500 citations with an h-index of 57 at present. Ravishankar is a fellow of several academies in India and abroad. He plays an active role in the International Union of Food Science and Technology and the Institute of Food Technologists of the USA, who have recognized him with the honor of fellow. He is widely traveled and has given invited talks in many international symposia and seminars. He has been a visiting professor to universities in Japan, Taiwan, and Russia.

This book is dedicated to Dr. Ravishankar Gokare A, for mentoring a large number of students including one of the authors, Dr. Ramakrishna, and several researchers, who are contributing immensely to the field of plant biotechnology for food application. His simplicity, humble behavior, kindness to colleagues, and positive outlook is exemplary. We sincerely hope that he will continue to make contributions of global relevance and to nurture young generation of researchers to be global leaders.

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Foreword

Not every scientist in the world has the basic skills to write and compile a comprehensive book on a challenging research area like *Metabolic Adaptations in Plants During Abiotic Stress*. Dr. Akula Ramakrishna and Dr. Sarvajeet Singh Gill completed this work remarkably. They have teamed up to cover all the burning topics and mechanics pertaining to metabolic adaptations of plants during the adverse and stressed conditions related to polyamines, indoleamines, antioxidative systems, adaptations in seeds under arid conditions, the roles of osmoregulators, secondary metabolites and miRNAs, kinase signaling, the impact of ozone and flavonoids, mechanisms and operating pathways during stresses, photoinhibitory responses, genomic response, antioxidant isoenzymes, management of heavy metal stress, pesticide stress, ATPases in ion homeostasis, genetic engineering approaches for abiotic stress tolerance in plants for sustainable agriculture, and food security. All these topics make this book wonderful and highly useful to the scientific community.

This book is worth reading for every student and scientist doing active research in agriculture and abiotic studies. Some of you may be wondering why I am praising this book. This book matters because our climate is changing, and the plant kingdom is seriously affected, which plays a significant role in the sustainability of human life and the whole ecosystem on Earth.

I strongly believe the content described here will be very useful for taking precautionary steps to sustain our agricultural system during upcoming adverse conditions.

This book provides a wide view of abiotic stress research materials to diversify each person's learning experiences. Students should cultivate new ideas by relating to the current research and knowledge described in simple and eloquent terms in each chapter. This thorough research should improve their knowledge and nurture their research productivity, as well stimulate incentives for further learning. This well-organized book provides an excellent opportunity for students, as well as for the whole scientific community.

I feel honored and privileged to have this opportunity to write a foreword to Dr. Ramakrishna and Dr. Gill's book. The challenges of abiotic stress in plant growth and development are evident, and the authors' dedication in this direction is appreciated. This is the area of future research that will help us all to thrive, along with plants.

Shashi Kumar, PhD

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Acknowledgments

Our special thanks and heartiest gratitude to all the contributors of this volume, who have provided an ample treatise on the topic. We understand that the contributors are active scientists and have agreed to share their findings and perspectives with the readers, who will benefit from learning about the implications and applications of the subject matter of the book as an emerging area of science.

We are grateful to Alice Oven (Senior Editor), Jennifer Blaise (Senior Editorial Assistant), Lara Silva McDonnell (Senior Project Manager), and the team from Taylor & Francis for their help in bringing out the volume in an attractive manner.

Both of us are thankful to our families who encouraged us to take up this task and permitted us to take the time off from our relationships.

Dr. Ramakrishna is thankful to Monsanto Crop Breeding Center, Bengaluru, for their support and also thankful to his mentors Dr. G.A. Ravishankar and Dr. P. Giridhar for their guidance. Dr. Ramakrishna also extends thanks to the staff and students of the Plant Cell Biotechnology Department, CFTRI, Mysore, India. Dr. Gill also acknowledges the unconditional support and guidance of Professor (Dr.) Narendra Tuteja, ICGEB, New Delhi.

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Editors



Dr. Ramakrishna Akula is currently a scientist at Monsanto Breeding Station, Bangalore, India. Dr. Ramakrishna holds a master's degree from Sri Krishna Devaraya University, Anantapur, India. He started his research career in 2005 at the Department of Plant Cell Biotechnology, CFTRI, Mysuru, in the research group of Dr. G.A. Ravishankar. He is a Senior Research Fellow of CSIR, New Delhi. He obtained his PhD in biochemistry from

University of Mysore, Mysuru, in the area of development of high frequency somatic embryogenesis and regulation of secondary metabolites in *Coffea canephora*. He worked extensively on the role of serotonin, melatonin, and calcium-mediated signaling in plants. He has made significant contributions to metabolic engineering of secondary metabolites from plants and abiotic stress in plants. He has worked in the area of tissue culture, *in vitro* production, and regulation of plant secondary metabolites from food value plants that include natural pigment caffeine, steviosides, anthocyanins, and carotenoids. He is the author of three books, 12 peer-reviewed publications, two reviews, and eight chapters in books. His books include *Serotonin and Melatonin: Their Functional Role in Plants, Food, Phytomedicine, and Human Health*, *Metabolic Adaptations in Plants During Abiotic Stress* (CRC Press, 2016) and *Neurotransmitters in Plants: Perspectives and Applications* (CRC Press, 2018). He is a member of the Society for Biotechnologists (India). He is a fellow of the Society for Applied Biotechnology, India (2012), and has received the Global Vegetable Research Excellence Award (2017), three global technology recognition awards, a Rapid Recognition Award, Test Master, Asia Veg R&D quarterly recognitions, and special recognition from the Monsanto company. He attended the Fifth International Symposium on Plant Neurobiology held in 2009 in Florence, Italy. He also attended the Technical Community of Monsanto (TCM) held in 2016, in St. Louis, Missouri.



Dr. Sarvajeet Singh Gill is currently working as assistant professor at the Centre for Biotechnology, Maharshi Dayanand University, Rohtak, Haryana, India. In 2001, Dr. Gill completed his MSc in Botany from Aligarh Muslim University, Aligarh, India, with Gold Medal. Soon after, Dr. Gill started his research career (M.Phil. and PhD, 2001–2008)

in plant stress physiology and molecular biology at AMU. Dr. Gill has made significant contributions towards abiotic stress tolerance in crop plants. Dr. Gill's research includes abiotic stress tolerance in crop plants, reactive oxygen species signaling and antioxidant machinery, gene expression, helicases, crop improvement, transgenics, nitrogen and sulfur metabolism, and plant fungal symbiotic interactions. Together with Dr. Narendra Tuteja at the International Centre for Genetic Engineering and Biotechnology (ICGEB), New Delhi, he worked on plant helicases for abiotic stress tolerance. He further explored the mechanism of stress tolerance by overexpressing PDH45 in tobacco and rice (*Plant Mol Biol* 82(1–2):1–22, 2013, and *PLoS One* 9(5):e98287, 2014). A novel function of plant MCM6 in salinity stress tolerance has also been reported that can will help to improve crop productivity at sub-optimal conditions (*Plant Mol Biol* 76(2011):19–34, 2014). Herbicide and salt stress tolerance (PDH45 + EPSPS) in plants has also been explored (*Front. Plant Sci.* 8:364, 2017). Dr. Gill helped to develop salinity-tolerant tobacco and rice plants, without affecting the overall yield. This research uncovers new pathways to plant abiotic stress tolerance and indicates the potential for improving crop production at sub-optimal conditions. A recipient of the INDIA Research Excellence & Citation Award 2017 from Clarivate Analytics (Web of Science), Sarvajeet Gill has edited several books with Springer, Wiley, Elsevier, CABI, and others, and has a number of research papers, review articles, and book chapters to his name.



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Section I

Abiotic Stress Management and Its Impact on Plants



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Effects of Different Abiotic Stresses on Primary Metabolism

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Salinity Stress

General Considerations of Salt Stress as a Global Problem

Salt stress is one of the major abiotic stresses that seriously affect crop growth and yield. According to the Food and Agriculture Organization FAO (2009), there are at least 800 million hectares of land subjected to salinity in the world, accounting for as much as 6% of the world's total area. Although some of the salt-affected influences are the result of natural causes, the majority are derived from degraded cultivated agricultural land (Tang et al., 2014). It is estimated that 30% of the world's irrigated areas already suffer from salinity problems (UNESCO Water Portal, 2007). Each year, soil salinity increases worldwide, and it is predicted that it will cause a loss of up to 50% of the cultivatable land by 2050 (Henry et al., 2015). Expansion of agriculture to semi-arid and arid regions with the use of intensive irrigation will increase secondary salinization as a result of changes in the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration). Moreover, the faster-than-predicted change in global climate (Intergovernmental Panel on Climate Change, 2007) and the different available scenarios for climate change suggest an increase

in aridity for the semi-arid regions of the globe in the near future. Together with overpopulation this will lead to an overexploitation of water resources for agriculture purposes and increased constraints on plant growth and survival; this will affect the ability to realize crop yield potential (Chaves et al., 2009).

The United States Department of Agriculture (USDA) Salinity Laboratory defines a saline soil as having an electrical conductivity of the saturation extract (EC_c) of 4 dS m⁻¹ or more. EC_c is the electrical conductivity of the saturated paste extract, that is, of the solution extracted from a soil sample after being mixed with sufficient water to produce a saturated paste. The most widely accepted definition of a saline soil has been adopted from FAO (1996) as one that has an EC_c of 4 dS m⁻¹ or more and soils with EC_cs exceeding 15 dS m⁻¹ are considered strongly saline. Traditionally, four levels of soil salinity based on saline irrigation water have been distinguished: low salinity is defined by electrical conductivity of less than 0.25 dS m⁻¹; medium salinity, 0.25–0.75 dS m⁻¹; high salinity, 0.75–2.25 dS m⁻¹; and very high salinity with an electrical conductivity exceeding 2.25 dS m⁻¹ (US Salinity Laboratory Staff, 1954). The common cations associated with salinity are Na⁺, Ca²⁺ and Mg²⁺, while the common anions are Cl⁻, SO₄²⁻ and HCO₃⁻ (FAO: Land and Water Division, 2013).

Saline stress in plants refers to the presence of neutral salts such as NaCl or Na₂SO₄ in soil, whereas alkaline stress is only

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related to the occurrence of alkaline salts: Na_2CO_3 or NaHCO_3 . These conditions often co-occur in nature, with variable neutral to alkaline salt proportions according to the soil (Paz et al., 2014). Since Na^+ in particular causes deterioration of the physical structure of soil and along with Cl^- is toxic to plants, these are considered the most important ions. Historically soils were classified as saline, sodic or saline-sodic based on the total concentration of salt and the ratio of Na^+ to Ca^{2+} and Mg^{2+} in the saturated extract of the soil (Yadav et al., 2011).

According to the incapacity to grow on high salt medium, plants have also been classified as glycophytes or halophytes. Most plants are glycophytes and cannot tolerate salt stress and in a large proportion of crops cannot tolerate Na^+ concentrations at 50 mM or higher (Tang et al., 2014). The deleterious effects of salinity on plant growth are associated with: (1) low osmotic potential of soil solution (water stress), (2) nutritional imbalance, (3) specific ion effect (salt stress) or (4) a combination of these factors (Parvaiz and Satyawati, 2008). Early plant responses to water and salt stress have been considered mostly identical; drought and salinity share a physiological water deficit that affects, more or less intensely, all plant organs (Munns, 2002). However, under prolonged salt stress plants respond in addition to dehydration to hyper-ionic and hyper-osmotic stress (Fricke et al., 2006). Na^+ and Cl^- are taken up and, increasingly, displace mineral nutrients such as K^+ , Ca^{2+} and nitrate (Campestre et al., 2016). Although accumulation of Na^+ and Cl^- causes osmotic and water potential adjustment of cells, it increases the risk of long-term ion toxicity. If Na^+ and Cl^- are not compartmentalized appropriately, exported or secreted, leaf tissue water deficit per se can be triggered not only by low soil water content but also by high vapor pressure deficit of the atmosphere (Chaves et al., 2016; Paz et al., 2014). Photosynthesis, together with cell growth, is among the primary processes to be affected by drought (Chaves, 1991) or by salinity (Munns et al., 2006). The effects can be direct, as the decreased CO_2 availability caused by diffusion limitations through the stomata and the mesophyll, and alterations of photosynthetic metabolism, or they can arise as secondary effects, namely oxidative stress. The latter are mostly present under multiple stress conditions and can seriously affect leaf photosynthetic machinery (Chaves et al., 2009).

In recent years, much attention has been devoted to the involvement of polyamines (PAs) as second messengers in the context of a variety of environmental stresses (Marina et al., 2008). These low-molecular-weight, aliphatic nitrogenous compounds, which are protonated at physiological pH, were originally thought to bind to anionic macromolecules, including proteins and nucleic acids, and thus to perform a structural role (Gárriz et al., 2003). The three commonest plant PAs, namely putrescine (Put), spermidine (Spd) and spermine (Spm), are now known; they protect salinity-stressed plants by aiding the accumulation of sugars, proline (Pro) and other osmolytes, and adjusting ion channels to maintain the plant's internal K^+ and Na^+ balance. They also serve to increase the activity of a range of antioxidant enzymes, thereby improving the plant's ability to control oxidative stress. The involvement of PAs in the response of higher plants to salinity stress has been widely reported (Zheng et al., 2016) and deserves to be mentioned, however, we focus in this chapter on plant primary metabolism and how different abiotic stresses affect it.

In recent years, tremendous advances have been achieved in salt stress studies. Plant breeders have fostered some salt-tolerant lines of crops by conventional breeding; moreover, a transgenic approach is employed to improve crop salt tolerance and a number of transgenic lines have been found to be effective under control conditions. Metabolomics is becoming a tool to understand the cellular mechanism of abiotic stress and acts as a viable option for the biotechnological improvement of halophytes (Tang et al., 2014). Nevertheless, the salt tolerance trait is a multigenic property and is related to physiological, biochemical and molecular processes, so genetic engineering to produce salt-tolerant crops is limited seriously in nature (Zhu, 2003). More energy, material and financial resources are needed to invest in research. Only in this way can the mechanisms and principles be discovered and corresponding solutions be proposed.

Growth and Crop Production under Salt Stress Conditions

The effect of salt on plant establishment has been assessed in maize, sorghum, rice, wheat and soybean. Osmotic stress resulting from drought or salinized soils can be disastrous for crop development (Westgate and Boyer, 1985). Both stresses have a common but not exclusive osmotic component. Salinity generates an immediate osmotic stress followed by later ion toxicity after continued exposure (Carillo et al., 2011). During stress conditions, plants need to maintain internal water potential below that of soil and maintain turgor and water uptake for growing. This requires an increase in osmosis, by uptake of soil solutes, synthesis of metabolic solutes or accommodation of the ionic balance in the vacuoles (Parvaiz and Satyawati, 2008). Growing or surviving in a saline soil imposes some costs: the cost of excluding salt by intracellular compartmentalization and of excreting it through salt glands. This cost, however, is relatively small in relation to that needed to synthesize organic solutes for osmotic adjustment (Munns, 2002).

As was mentioned before, plants have been classified as glycophytes or halophytes. Most plants are glycophytes and cannot tolerate salt stress (Parvaiz and Satyawati, 2008). Nevertheless, important differences exist in salt tolerance between species. In most plants, higher levels of the activity of antioxidant enzymes are considered as salt tolerance mechanisms (Ashraf, 2009; Zhang et al., 2014). Indeed, previous studies have shown that within the same species, salt-tolerant cultivars generally have higher constitutive or enhanced antioxidant enzyme activity under salt stress when compared with salt-sensitive cultivars. This has been demonstrated in numerous plant species such as cotton (*Gossypium herbaceum*), rice and pea. Moreover, the response of plant antioxidant enzymes to salinity has been shown to vary among plant species, tissues and subcellular localizations (Mittova et al., 2003). Dramatic variances are found between plant species production in saline versus control conditions over a prolonged period of time. For example, after some time in 200 mM NaCl, a salt-tolerant species such as sugar beet (*Beta vulgaris*) might have a reduction of only 20% in dry weight, a moderately tolerant species such as cotton might have a 60% reduction, and a sensitive species such as soybean might be dead (Greenway and Munns, 1980). In very salt-sensitive species, salt-specific effects can become visible after several days at high salinities. If the salinity is high, and if the

plant has a poor ability to exclude NaCl, marked injury in older leaves might occur within days, as found for white lupin (*Lupinus albus*) once the salinity increased above 100 mM NaCl (Munns, 1988). *Medicago sativa* plants showed after 4 and 6 weeks of salt treatment a biomass reduction of about 40% and 50% with 150 mM NaCl, respectively (López-Gómez et al., 2014). At first the growth reduction is quickly apparent, and is due to the salt outside the roots. It is essentially a water stress or osmotic phase, for which there is surprisingly little genotypic variation (Munns, 2002). The growth reduction is presumably regulated by hormonal signals coming from the roots. Then, there is a second phase of growth reduction, which takes time to develop, and results from internal injury. This internal injury is due to Na⁺ or Cl⁻ (or both) accumulating in transpiring leaves to excessive levels, exceeding the ability of the cells to compartmentalize these ions in the vacuole. Ions then build up rapidly in the cytoplasm and inhibit enzyme activity or they build up in the cell walls and dehydrate the cell (Flowers and Yeo, 1986). This process inhibits the growth of the younger leaves by reducing the supply of carbohydrates to the growing cells (Munns, 2002).

Evidence indicates that plants have two phases of growing response that have been shown clearly, for example, for maize and wheat cultivars. Two maize cultivars with two-fold differences in rates of Na⁺ accumulation in leaves had the same growth reduction for 15 days in 80 mM NaCl. Furthermore, another two maize cultivars, again with two-fold differences in Na⁺ accumulation, had the same growth reduction for 4 weeks in 100 mM NaCl, and it was not until 8 weeks of salinity that a growth difference was clearly observed (Munns, 2002).

Differences are evident between the phenotype given by salt-stressed maize plants versus control irrigated only with nutritive solution (Henry et al., 2015). Similar results were found in wheat (Munns et al., 1995). Maize plants are most susceptible during a period of 2 weeks around the time of silking, and kernel abortion is the limiting factor for yield (Boyer, 2010). Recent studies identify events as early as 1 day after pollination to be critical for determining whether the embryo will abort (Chaves et al., 2003). With rice, also, a clear distinction has been made between the initial effects of salinity, which are recoverable, and the long-term effects that result from the accumulation of salt in the expanded leaves (Yeo et al., 1991).

In general, in the first few seconds or minutes of salt stress exposure, plant cells lose water and shrink. Then, cells regain their original volume but cell elongation rates are reduced, leading to lower rates of leaf and root growth. Over a number of days, changes in cell elongation and cell division lead to slower leaf appearance and smaller final size, and leaf growth is usually more affected than root growth (Munns, 2002). Root ionic status does not increase with time, as in leaves, and they often have a lower Na⁺ and Cl⁻ concentration than the external solution, which rarely happens in leaves. For example, in wheat growing in 150 mM NaCl, Na⁺ in the roots was only 20–40 mM (Gorham et al., 1990). In plants with high salt uptake rates, the oldest leaf may start to show symptoms of injury. After months, differences between plants with high and low salt uptake rates become very apparent, with a large amount of leaf injury and complete death in some cases if the salinity level is high enough (Munns, 2002).

In maize, kernel abortion induced by osmotic stress correlates with reduced evapotranspiration and photosynthesis (Setter and

Flannigan, 2001). Along with impaired photosynthesis in source leaves comes a reduction of seed sink strength. Abortion caused by osmotic stress correlates with depleted sucrose and reduced sugar levels, reduced sucrose degrading enzyme activity and transcript levels, and depletion of starch in the kernels (Henry et al., 2015). These events occur in a short period of time around pollination and can be partially prevented by stem sucrose feeding (Boyer, 2010). As a result of impaired photosynthesis and sink strength, sugar allocation to the reproductive organs is disrupted and the young embryo rapidly starves and aborts. Sugars not only serve as a source of carbon units and metabolic energy but also function as signaling molecules reporting carbon status within the cell (León and Sheen, 2003; Henry et al., 2015).

Seedling stage is the more vulnerable phase of durum wheat (*Triticum durum*) growth under salinity (Carillo et al., 2008). This species is more sensitive to salinity than bread wheat (*Triticum aestivum*) and poor yields on saline soil are partly due to the poor ability of durum wheat to exclude sodium (Annunziata et al., 2017). In particular, salinity greatly increases the levels of proline and glycine betaine (GB) in durum wheat (Munns, 2002; Carillo et al., 2008), as in other Poaceae. In many halophytes, leaf concentration of Pro, GB or both contributes to the osmotic pressure in the cell as a whole. In glycophytes, proline and GB have lower concentrations but, being partitioned exclusively to the cytoplasm, which makes up about 10% of the volume of the cell, they are able to determine significant osmotic pressure and balance the vacuolar osmotic potential (Annunziata et al., 2017).

The effect of salinity on the germination, vegetative growth and yield of cotton has also been reported (Ahmads et al., 2002; Guo et al., 2012). Cotton is classified as a salt-tolerant crop, but this tolerance is actually limited and varies according to the growth and developmental stages of the plant. Breeders have sought to make cotton more tolerant to salt through various methods, including traditional plant breeding and biotechnological approaches such as creating transgenic cotton (Chen et al., 2016). The growth rates of cotton plant roots and leaves decrease with increasing salt concentration, which may be a result of osmotic injury or specific ion toxicity (Meloni et al., 2001). Salt stress significantly reduces the growth rates in surface area, volume, average diameter of the cotton roots, and dry weights of roots and leaves (Zhang et al., 2014). This is accompanied by strong changes in carbohydrate metabolism owing to severe impairments in the photosynthetic and respiration apparatus (Chen et al., 2016).

On the other hand, legumes are classified as salt-sensitive crop species and their productivity is particularly affected because nodular nitrogenase activity markedly decreases upon exposure to mild saline conditions (Läuchli, 1984; López-Gómez et al., 2014). Salinity stress reduces seed germination, seedling growth, nodulation, biomass accumulation and seed yield (Essa, 2002). López-Gómez et al. (2014) have studied *M. sativa* and determined that nitrogenase activity is strongly inhibited by 150 mM NaCl 2 weeks after treatment initiation. The glycophyte *Lotus tenuis* (Waldst and Kit, syn. *L. glaber*; Kirkbride, 2006) is the best-adapted legume forage in the lowlands of the Buenos Aires Province (the most important cattle production region in Argentina) and is also affected by salt stress. The negative effect of NaCl on root length of *L. tenuis* is in agreement with previous results (Echeverría et al., 2008) along with important levels

of growth inhibition on its shoots that significantly decrease persistence and yield (Mazzanti et al., 1986; Paz et al., 2014). Singleton and Bohlool (1983) showed that nodule function was relatively more resistant to salt stress than plant growth. High soybean yields require large amounts of nitrogen (N); the least expensive source of N for soybean is biological fixation of atmospheric N_2 by the symbiotic association between plant and soil bacteria belonging mainly to the genera *Bradyrhizobium* and *Sinorhizobium*, which are collectively called soybean rhizobia. Rhizobia infect the roots of legumes and induce formation of nodules, where nitrogen fixation takes place (Baghel et al., 2016). Similarly to the nitrogenase activity, nodule dry weight was also reduced by salt treatments particularly in the case of *M. sativa* in which 35% and 50% of reduction was obtained by 100 and 150 mM NaCl after 2 weeks (López-Gómez et al., 2014).

Owing to the high oil and protein content in its seeds, soybean is an important economic dicot crop and the demand for it is increasing continuously. However, as a salt-sensitive species, the growth and development are severely affected by salt stress. Exploiting resistant varieties and improving salt tolerance of soybean, therefore, became the goal of many researchers (Chen et al., 2011). In mature seedlings of cultivated soybean (*Glycine max*), the water potential was reduced 11.2 times and the relative water content dropped to 64.2% under 300 mM treatment. In addition, all the plants under this stress displayed symptoms of water loss and 30% died after the stress. For young seedlings the accumulation of Pro increased rapidly when the concentration of the NaCl reached 100 mM or higher. Under 300 mM, the contents of the Pro reached 34.4 times. Previous studies on the synthesis and degradation of Pro have proved a close relationship between Pro and salt resistance. GB was another important metabolite playing an important role in salt resistance and its behavior was similar to Pro (Wu et al., 2014). The Pro content in the cotyledons of the 4-day-old germinating soybeans increased in the plants subjected to NaCl stress as well as the gamma-aminobutyric acid (GABA) content (Yin et al., 2015).

Plant Chemical and Physical Response to Salt Stress

An efficient response to the environment is particularly important for plants, as sessile organisms. This means an ability of cells to quickly sense the surrounding environmental signals. Systemic signals generated by the tissue exposed to abiotic and biotic stress act in the co-ordination and execution of plant stress responses in terms of metabolic and developmental adjustments (Chaves et al., 2003). Under salt and drought, these responses are triggered by primary osmotic stress signals, which have an impact on both the source of carbohydrate (photosynthesis) and the mobilization/utilization of carbohydrate reserves (sink strength), or by secondary signal metabolites that generally increase or decrease in a transient mode. The latter include hormones (e.g. abscisic acid (ABA), ethylene, cytokinins), reactive oxygen species (ROS) and intracellular second messengers, e.g. phospholipids, sugars, etc. (Chaves et al., 2003). Salt stress signaling consists of ionic and osmotic detoxification and signaling to coordinate cell division and enzyme expansion. Several salt-responsive signaling pathways, such as salt overly sensitive (SOS), ABA, Ca^{2+} signal transduction, protein kinase, phospholipid, ethylene and

jasmonate acid (JA) induced signaling pathways, have been predicted (Zhang et al., 2012).

Stomata close in response to leaf turgor decline, high vapor pressure deficit in the atmosphere (Chaves et al., 2009) and early physiological events such as root-generated chemical signals. A close relationship is usually found between stomata conductance (G_s) and net CO_2 assimilation (A_N) (Flexas et al., 2004); photosynthesis rate is affected by salt stress directly due to CO_2 deficiency and Rubisco (RuBP) activity, and indirectly by reduced chlorophyll and total carotenoid content (Tang et al., 2014).

Since roots are the site of perception of salt in the environment, their responses and adaptive behavior form the first line of defense against stress damage (Ji et al., 2013). High concentrations of NaCl outside the roots reduce the water potential and make it more difficult for the root to extract water (Zhang et al., 2014). Sodium exclusion by root cells is the primary protecting response in plants that delays the toxic effects of high cytoplasmic Na^+ . The comparison of unidirectional Na^+ uptake fluxes and the rates of net accumulation of Na^+ in roots indicate that the vast majority of the Na^+ taken up into the root symplast is extruded back to the apoplast and soil solution (Ji et al., 2013). Proper regulation of ion flux is necessary for cells to keep the concentrations of toxic ions low and to accumulate essential ions. Plant cells employ primary active transport, mediated by H^+ -ATPases (Yokoi et al., 2002) that create a proton-motive force that drives the transport of all other ions and metabolites; and a secondary transport, mediated by channels and co-transporters, to maintain characteristically high concentrations of K^+ and low concentrations of Na^+ in the cytosol (Parvaiz and Satyawati, 2008).

The cytoplasm also accumulates low-molecular-mass compounds commonly called compatible solutes that do not interfere with normal biochemical reactions; rather, they replace water in biochemical reactions. While some compatible osmolytes are essential elemental ions (such as K^+) (Xiong et al., 2002), the majority are organic solutes (Zhu, 2003). However, the solutes that accumulate vary with the organism and even between plant species. A major category of organic osmotic solutes consists of simple sugars (mainly fructose and glucose), sugar alcohols (glycerol and methylated inositols) and complex sugars (trehalose, raffinose and fructans). Carbohydrates (glucose, fructose, sucrose, fructans) and starch accumulate under salt stress, playing a leading role in osmoprotection, osmotic adjustment, carbon storage and radical scavenging (Parvaiz and Satyawati, 2008). Others include quaternary amino acid derivatives (proline, glycine betaine, β -alanine betaine, proline betaine, tertiary amines 1,4,5,6-tetrahydro-2-methyl-4-carboxyl pyrimidine) and sulfonium compounds (choline O-sulfate, dimethyl sulfonium propionate) (Bohnert and Jensen, 1996; Yokoi et al., 2002).

Under mild stress, a small decline in stomata conductance may have protective effects against stress, by allowing plants to save water and improving plant water-use efficiency. The result of closing stomata is the reduction of CO_2 diffusion. There is an increasing body of evidence that shows g_m (internal leaf conductance to CO_2 diffusion) decreases in response to drought and salinity (Flexas et al., 2004). These changes in mesophyll conductance may be linked to physical alterations in the structure of the intercellular spaces due to leaf shrinkage or to alterations in the biochemistry (bicarbonate to CO_2 conversion) and/or membrane permeability (aquaporins) (Chaves et al., 2009).

The cell cortex is a specialized layer of the cytoplasm underlying the plasma-membrane that is composed of a network of microtubules and actin filaments. Cortical microtubules are highly dynamic and remodeled by numerous stimuli. Salt stress induces dynamic cytoskeletal changes, with initial depolymerization of microtubules at the onset of stress followed by repolymerization. Both depolymerization and reorganization of the cortical microtubules are important for the plant's ability to withstand salt stress (Ji et al., 2013).

Changes in leaf biochemistry that result in down-regulation of the photosynthetic metabolism may occur in response to lowered carbon substrate under prolonged stresses (Flexas et al., 2006). A deactivation of the carboxylating enzyme RuBP by low intercellular CO₂ has been observed along with other important photosynthetic proteins that are down-regulated by different mechanisms (carbonylation, phosphorylation/dephosphorylation and redox changes in thiol groups). These salt-induced alterations may induce great disturbances in photochemical activity, decreasing the growth and increasing salt plant sensitivity (Henry et al., 2015; Silveira and Carvalho, 2016). There is a large amount of data on initial RuBP activity and only one study in which nitrate reductase activity was followed concomitantly with Gs during a drought cycle. Even so, it seems clear that both enzymes share a common pattern on regulation with decreasing Gs. The fact that initial RuBP activity remains unaffected from maximum Gs down to 0.1 mol H₂O m⁻² s⁻² implies that within this range, photosynthesis is not impaired by the carboxylation capacity (Flexas et al., 2004). Early biochemical effects that involve alterations in photophosphorylation (a decrease in the amount of ATP leading to a decreased regeneration of Rubisco) have also been described (Tezara et al., 1999) and seem to be dependent on species showing different thresholds for metabolic down-regulation (Lawlor and Cornic, 2002).

Under salt stress, metabolic limitations of photosynthesis resulting from increased concentrations of Na⁺ and Cl⁻ in the leaf tissue (in general above 250 mM) do occur (Munns et al., 2006). As previously pointed out, the fast changes in gene expression following stress imposition that have been observed suggest that alterations in metabolism start very early. Although its role is not totally clear yet, photorespiration may also be involved in protecting the photosynthetic apparatus against light damage as suggested by its increase under drought observed in several species. Photorespiratory-produced hydroxide peroxide (H₂O₂) may also be responsible for signaling and acclimation under restricted CO₂ availability (Noctor et al., 2002). Several lines of evidence suggest that stomatal closure in moderately salt-stressed leaves leads to enhanced rates of photorespiration. The following parameters, all indicative of higher rates of photorespiration, have been shown to increase: the CO₂ compensation point, the light to dark ratio of CO₂ production, the stimulation of photosynthesis by lowering the O₂ concentration, the activity of glycolate oxidase and the formation of photorespiratory metabolites, such as glycine, serine and glycolate. The maintenance of considerable rates of electron transport in CO₂-free air also indicates a significant occurrence of photorespiration in salt-stressed leaves. In addition to sustained rates of electron transport due to photorespiration, the formation of zeaxanthin (one of the most common carotenoid alcohols found in nature) also mitigates against

photo inhibitory damage, although this protection by zeaxanthin is not complete in high light (Wingler et al., 2000).

Salt-tolerant plants can not only regulate ion and water movements more efficiently but should also have a better antioxidant system for effective removal of ROS (Noctor et al., 2002). Molecular oxygen in its ground state, triplet oxygen, is essential to life on earth. It is a relatively stable molecule that does not directly cause damage to living cells. However, when triplet oxygen receives extra energy or electrons, it generates a variety of ROS that will cause oxidative damage to various components of living cells including lipids, proteins and nucleic acids (Abogadallah, 2010). Salt stress causes excessive generation of ROS: singlet oxygen (¹O₂), hydrogen peroxide (H₂O₂), superoxide anions (O⁻²) and hydroxyl radicals (OH•). To mitigate the oxidative damage initiated by ROS formed under salt stress, plants possess a complex antioxidant system, including non-enzymatic antioxidants such as ascorbic acid, glutathione, tocopherols and carotenoids; antioxidant enzymes such as superoxide dismutase, catalase, glutathione peroxidase and enzymes of the so-called ascorbate-glutathione cycle, including ascorbate peroxidase and glutathione reductase (Zhang et al., 2014). Plants produce ROS under normal conditions essentially from photosynthesis, photorespiration and respiration. The most common ROS generated under normal conditions are O⁻² and H₂O₂ perhaps as a result of electron leakage from the photosynthetic and respiratory electron transport chains to oxygen. Another source of ROS (H₂O₂) is photorespiration resulting from the oxygenase activity of RuBP. Rates of photorespiration are basically controlled by the ratio of [CO₂] to [O₂] and temperature. In C₃ plants, photorespiration constitutes about 20%–30% of photosynthesis under the current atmospheric conditions at 25°C. In contrast, C₄ plants show lower rates of photorespiration (3.5%–6% of photosynthesis) under various environmental conditions due to their CO₂ concentrating mechanism. The role of ROS detoxification under salt stress may have resulted at least in part from (1) the technical inability to determine the major sources(s) of ROS under salt stress and therefore the appropriate antioxidant enzyme required and (2) the expectation that ROS scavenging enzymes, particularly catalases and peroxidases, perform similar functions (Abogadallah, 2010).

Salinity can affect growth in a number of ways. The first phase of the growth response is due to the osmotic effect of the salt in the soil solution and produces a suite of effects identical to those of water stress caused by drought. Later, there may be an additional effect on growth; if excessive amounts of salt enter the plant they will eventually rise to toxic levels in the older transpiring leaves, causing premature senescence. This will reduce the amount of assimilate that the plant can produce, and a reduction in assimilate transported to the growing tissues may further limit growth. This is the second phase of the growth response and is the phase that clearly separates species and genotypes that differ in the ability to tolerate saline soil (Munns, 2002). In summary, in order to guarantee survival under such detrimental circumstances, plants have evolved a series of biochemical and molecular processes to acclimatize themselves to the environment (Yan et al., 2013). The specific biochemical strategy contains: (1) ion regulation and compartmentalization, (2) induced biosynthesis of compatible solutes, (3) induction of antioxidant enzymes, (4) induction of plant hormones and (5) changes in photosynthetic

pathway. The molecular mechanism includes: (1) the salt overly sensitive (SOS) pathway for ion homeostasis, (2) the protein kinase pathway for stress signaling, (3) the phytohormone signaling pathway under high salt stress and (4) the associated genes encoding salt-stress proteins, such as genes for photosynthetic enzymes, synthesis of compatible solutes, vacuolar-sequestering enzymes and for radical-scavenging enzymes (Tang et al., 2014).

The accumulated knowledge on physiological, cellular and molecular responses of plants to drought and salinity, including the signaling events occurring under both stresses, is already permitting great progress in crop management and breeding (Chaves et al., 2009). Some improvement in plant stress tolerance has been achieved by introducing stress-inducible genes into some model plants. To further understand the complexity of plant response to drought and salt, including the effects on photosynthesis, is important to strengthen multilevel genomics and physiological studies, covering different intensity and timing of imposition of the stresses in genotypes with different sensitivity to stress.

Cold Stress

Effect of Cold Stress on Primary Plant Metabolism

Climatic changes affect the normal performance of the plant. Low temperatures cause damage in different physiological stages (seedling, reproductive stage and grain filling), resulting in a reduction in crop yield. Low temperatures are a major environmental factor limiting the productivity and the geographic areas where agriculture can be developed.

Changes in environmental conditions make plants reprogramme metabolic fluxes because cold temperatures produce high metabolic requirements to maintain normal physiological processes. Chilling treatments of sensitive tissues increases the activity of invertase, catalase, pyruvate decarboxylase, glucose-6-phosphate dehydrogenase and phosphoenolpyruvate carboxykinase. Likewise, decreases have been observed in a number of systems including malate dehydrogenase and amylase (Lyon, 1973).

Plants that have evolved with mechanisms of tolerance and adaptation to cold have C_3 type photosynthesis and rapidly mobilize the reserves stored. Moreover, changes in starch metabolism and raffinose family oligosaccharide synthesis are all participants in the global response to cold stress (Janska et al., 2010).

Accumulations of soluble sugars from the hydrolysis of starch (Chen et al., 2014) and their roles in stabilizing biological components, particularly for raffinose family oligosaccharides (RFO) (Tarkowski and Van den Ende, 2015), are much-studied processes in plant physiology to understand the effects of cold and cold acclimation.

It has been reported that the accumulation of galactinol assimilates such as glucose, fructose and sucrose, as well as changes in the biosynthesis of protein lipids, are adopted strategies for cold stress tolerance in plants; these act as cryoprotective molecules (Rodziewicz et al., 2014).

In C_4 plants such as maize (*Zea mays*), the leaf structure minimizes photorespiration, which is a major source of ROS in C_3 plants (Foyer, 2002).

Changes in environmental conditions such as cold temperatures associated with light energy result in an imbalance between the light energy absorbed through photochemistry versus the

energy utilized through metabolism, which reflects the relative reduction state of the photosystem, generating ROS. This acts as a signal to influence the nuclear expression of a specific cold-acclimation gene (Huner et al., 1998).

Photosynthesis and Carbon Metabolism

Several authors have shown that the rate of photosynthesis decreases in higher plants during exposure under low temperatures. This reduction is due to stomatal closure and the consequent disability for CO_2 fixation. On the other hand, cold temperatures bring about photoinhibition of photosystem II (PSII) caused by the enhanced production of reactive oxygen species damaging the photosynthetic machine.

The key enzyme for CO_2 incorporation is ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBP). It has been postulated that in seedlings subjected to cold, large RuBP subunits and RuBP-binding protein were downregulated, which may suggest chloroplast damage (Rodziewicz et al., 2014). Furthermore, it has been shown in rice (*Oryza sativa*) seedlings that synthesis of RuBP is drastically reduced after cold exposure (Hahn and Walbot, 1989). In wheat (*Triticum aestivum*) exposed to prolonged cold, stress fragmentation of RuBP was also evidenced in proteomics profile; it was suggested that RuBP proteolysis causes sugar accumulation during cold exposure (Rinalducci et al., 2011).

Regardless of the phenological state of the plant (vegetative or reproductive), cold-sensitive wheat is affected as photosystem proteins and protein related to electron transport are down-regulated, causing alterations in the flow of electrons in the chloroplast (Rinalducci et al., 2011; Xu et al., 2013). These proteins were enhanced in cold-tolerant wheat (Xu et al., 2013).

However, in rice seedlings, the proteins related to the generation of energy and sugar biosynthesis are activated under conditions of cold temperatures (Makoto Hashimoto and Komatsu, 2007).

The transcriptomics profile of rice seedling reveals that the genes involved in photosynthetic processes PSI and PSII were down-regulated (Kyonoshin Maruyama et al., 2014). RNA sequencing studies in the legume *Lotus japonicus* subjected to growth at low temperatures also show down-regulation in genes corresponding to energy metabolism that affect the photosynthetic process and chloroplast development (Calzadilla et al., 2016). In soybean (*Glycine max*), comparative proteomic analysis of seedling leaves of cold-tolerant and -sensitive cultivars indicated that cold stress also affects photosystem proteins, indicating the tolerance is caused by less energy depletion in the tolerant cultivar (Tian et al., 2015). The same result was found in maize seedling where a proteomics profile based in i-TRAQ revealed which proteins are involved in photosynthesis; light harvesting and light reaction are down-regulated (Wang et al., 2016).

On the other hand, the opposite results were obtained in cold-tolerant soybean seed germinates exposed to $4^\circ C$, where the proteomic profile revealed an increase in most proteins linked to energy metabolism (Cheng et al., 2010).

The Role of Carbohydrates in Response to Cold Stress

Plants produce biochemical changes in response to low temperatures as a mechanism of adaptation and defense. A transition occurs when the metabolism of starch is directed towards

a metabolism aimed at accumulating oligosaccharides as cryoprotectants giving an osmotic adjustment response (Janska et al., 2010; Beck et al., 2007; Xiong and Zhu, 2002; Guy et al., 1992).

It could be said that this increase in the amount of sucrose, like a storage carbohydrate, is because it can be easily remobilized depending on the metabolic needs under stress conditions (Guy et al., 1992).

In wheat plants, seedling and reproductive stage exposed to chilling showed an increase in soluble carbohydrates (Savitch et al., 2000; Vargas et al., 2007; Rinalducci et al., 2011; Xu et al., 2013), especially sucrose, and an increase in the capacity for sucrose utilization through the biosynthesis of fructans, accompanied by an induction of the activity of the enzyme invertase, exhibiting a regulation mediated by free sugars in response to the cold (Savitch et al., 2000; Vargas et al., 2007). The same regulation was observed in legume nodules of *Lotus japonicus* in non-stressing conditions, indicating a possible role of invertases in producing hexoses for starch production when the metabolic requirements are high (Flemetakis et al., 2006).

RNA sequencing in seeds of tolerant indica rice detected high expression in enzymes involved in the synthesis of sucrose and breakdown of polysaccharides to generate simple sugars, such as glucose, compared to cold-sensitive indica rice (Dametto et al., 2015).

Comparisons between two soybean cultivars (tolerant and sensitive) in seedling stage reveal that cold stress affects the total amount of soluble carbohydrates, decreasing in both cultivars. At the same time, the protein profiles show a reduction in pentoses phosphate and glycolysis pathways for both cultivars (Tian et al., 2015). Other reports in seed soybean showed that proteins associated with carbohydrate enhanced starch metabolism as well as increasing the granule-bound starch gene (Cheng et al., 2010). In *Lotus japonicus* those genes of starch and sucrose metabolism also showed up-regulation (Calzadilla et al., 2016). In maize, most of the proteins associated with carbohydrate metabolism were accumulated after the chilling stress (Wang et al., 2016).

Metabolome analyses in rice seedling treated under low temperature revealed that levels of monosaccharides increased, while transcriptomics analyses indicated that several genes encoding enzymes involved in starch degradation, sucrose metabolism and the glyoxylate cycle are upregulated and that these changes are correlated with the accumulation of glucose, fructose and sucrose. In particular, high expression levels of genes encoding isocitrate lyase and malate synthase in the glyoxylate cycle correlate with increased glucose levels (Maruyama et al., 2014). In the reproductive stage of rice (booting stage) the starch and sucrose contents in the leaf blades and stems after panicle initiation did not undergo significant changes and carbon availability from source tissues is unlikely to affect chilling sensitivity in spikelet at the booting stage (Suzuki et al., 2015). Different results were reported in three maize inbred lines where a decrease in sucrose and glucose levels was found when analyzed by metabolism profile (Sun et al., 2016).

In another important forage legume, when two cultivars (*Medicago sativa* and *Medicago falcata*) were compared, both showed sugar accumulation (sucrose, galactinol and raffinose), although *M. sativa* displaying show accumulation of sugars. In *M. falcata* all sugars accumulated rapidly and stayed at high levels except for raffinose (Zhuo et al., 2013).

The raffinose family oligosaccharides (RFOs) are synthesized from sucrose by the subsequent addition of activated galactinol moieties donated by galactinol (ElSayed et al., 2014). Raffinose was accumulated in leaves accompanied by an increase in galactinol (Saito et al., 2011). It has also been observed that levels of transcripts of raffinose synthase decreased under cold stress but are increased under dehydration conditions (Maruyama et al., 2014).

Microarray analysis of rice plant at booting stage revealed that cold treatments during vegetative growth provoked up-regulation of a raffinose synthase gene, showing the same pattern as the heat shock protein genes (Suzuki et al., 2015). It has been proposed that higher levels of raffinose synthase, as well as raffinose, can assist in osmotic adjustments as well as in membrane and protein stabilization and to protect plants from oxidative stress caused by cold stress (Suzuki et al., 2015; ElSayed et al., 2014). Furthermore, there is evidence that in some plant species, change in RFOs is part of a mechanism for carbon storage rather than protection against environmental changes (ElSayed et al., 2014). Transcriptional up-regulation of the raffinose oligosaccharide pathway results in accumulation of monosaccharides and disaccharides, including glucose, fructose, sucrose, galactinol and raffinose (Jansko et al., 2010).

Higher levels of the transcript of the galactinol synthase encoded gene (MfGolS1) were induced and maintained in *M. falcata* than in *M. sativa* during cold acclimation, in accordance with the accumulation of sugars and the differential cold tolerance between *M. falcata* and *M. sativa* (Zhuo et al., 2013).

Galactinol synthase is the enzyme that catalyzes the first step of RFOs. Transgenic tobacco that overexpresses the exogenous gene MfGolS1 of *M. falcata* turned out to be more tolerant to freezing and chilling (Zhuo et al., 2013).

Trehalose is another nonreducing disaccharide that serves as a protector against stress. Trehalose synthesized via a phosphorylated intermediate, trehalose 6-phosphate (Tre6P), has been a reporter that the gene of trehalose-6-phosphate (TPS) increases in freezing stress (Song et al., 2016a). There is a strong correlation between sucrose and Tre6P. Parallel changes in their levels indicate that synthesis and degradation of Tre6P may be regulated by sucrose (Lunn et al., 2014). The demand for starch is regulated by sucrose-dependent changes in Tre6P that modulate the rate of starch breakdown according to the demand for sucrose (Lunn et al., 2014).

An accumulation of trehalose may act as a regulator of stress, giving greater tolerance under low temperatures. Transgenic rice plants which contained the exogenous gene trehalose biosynthetic (otsA and otsB) from *Escherichia coli* exhibited constant plant growth, less photo-oxidative damage and more favorable mineral balance under low-temperature stress conditions (Garg et al., 2002).

Fatty Acid Metabolism

Fatty acids are components of cellular membrane, thylakoid membrane and cutin waxes; trienoic fatty acids (TAs), hexadecatrienoic acid (16:3) and linolenic acid (18:3) are the major polyunsaturated fatty acid species in membrane lipids (Upchurch, 2008), and changes in their regulated plant response against low temperatures. Cold temperatures cause damage to the lipid

membrane; these oxidative lipid injuries are generated by ROS resulting in lipid peroxidation and changes in lipid compositions.

In physiological conditions, the membrane lipid is in the liquid crystal phase, but under low-temperature stress, it is transformed from the liquid phase into the gel phase, thus increasing the permeability of the membrane (Lyons, 1973; Chen et al., 2014; Tarkowski and Van den Ende, 2015). This arrangement of membrane fluidity, with the transition to gel phase, is accompanied by an increase in the proportion of unsaturated fatty acids (Beck et al., 2007; Janska et al., 2010; Chen et al., 2014).

Releasing α -linolenic acid (18:3) is a way of modulating the membrane flow, in chloroplast saturated phosphatidylglycerol (PG), with saturated fatty acids (16:0, 18:0) playing a key role in acclimatization of plants under chilling. Increased TAs in the plasma membrane enhance low-temperature tolerance in plants during the early growth stage (Iba, 2002; Upchurch, 2008).

The chloroplast is a sensitive target of low temperatures; differences between lipid compositions in chloroplasts may be the cause of plant sensitivity or tolerance to cold stress. The content of PGs in chloroplasts is 16:0 or 16:1; in tolerant plants the levels of 16:0, 16:1 and 18:1 are less than in sensitive plants (Iba, 2002).

Alfalfa studies comparing tolerant and cold-sensitive varieties showed that low-temperature-resistant varieties contained a higher percentage of polyunsaturated fatty acids in chloroplast membranes (Peoples et al., 1978).

Willemot (1977) described that saturated fatty acids at low temperature in wheat are not related to frost hardiness. Furthermore, in alfalfa it has been shown that linoleic acid accumulates at low temperature while wheat accumulates linolenic acid. In rice there is a positive relationship between the unsaturated fatty acid composition of the chloroplast membrane and the photosynthetic tolerance to chilling (Zhu et al., 2007).

A metabolome study in maize showed that triacylglycerides and diacylglycerides produced from the glycerolipid metabolic pathway significantly decreased when plant seedlings were exposed to low temperatures (Sun et al., 2016). In soybean, protein profiles comparing a sensitive and tolerant variety show that the low-temperature-tolerant cultivar improves the biosynthesis of fatty acids (Tian et al., 2015).

RNA sequencing in rice and lotus reveals that in sensitive plants there is a down-regulated gene in the metabolic lipid pathway (Dametto et al., 2015; Calzadilla et al., 2016). This indicates this is a generalized response in plants against cold stress where a regulation metabolic process exists related to unsaturated fatty acid accumulation.

Summary

There is a general response for plants against cold stress. The metabolic changes focus on counteracting the oxidative stress in the chloroplast and lowering the photoinhibition, particularly regulating the photosynthesis and carbohydrate metabolism.

The biochemical response produced by cold damage is generally associated with the accumulation of unsaturated fatty acids in order to decrease lipid peroxidation. Sugar accumulation, seems to be a response to support growth under temperature stress, acting like photoprotective molecules, lowering levels of ROS, and like osmotic molecules, regulating the osmotic imbalance caused by the cold. This mechanism is summarized in Figure 1.1.

As a strategy for future breeding projects it is thought that a plant phenotype that is more energy efficient at the level of chloroplast would lower the levels of ROS produced by the cold and the consequent photoinhibition. This would make the plant more metabolically efficient where the biochemical processes are geared towards growth rather than repair of damage, resulting in a greater grain yield in crop species.

Water Deficit

Plants Water Balance

Plant water balance explains the behavior of plants in terms of how they control the hydration of their cells, which has important implications in the physiological and metabolic processes that determine the quantity and quality of plant growth (Passioura et al., 2010). The plant water balance is determined by the ratio between the fraction of water lost in evaporation (transpiration) to the atmosphere and its absorption from the soil. When transpiration exceeds absorption, the relative water content (RWC) and the cellular volume decrease, determining the loss of cell turgor and at the same time increasing the solute levels in the cell, so osmotic potential (π) and water potential (ψ) fall (Lawlor and Cornic, 2002). This situation could be modified by osmotic adjustment (OA) in species that have such a defense mechanism. OA has been and is well established as a major regulator of turgor and stomata conductance (G_s) in drought (Blum, 2016). Turner and Jones (1980) indicate that OA was effective in sustaining turgor, RWC and G_s at low leaf water potential in sorghum. A lower state of cell turgor and RWC causes slow growth and G_s . In this context two parameters describe the water status of plants: RWC and ψ (Nobel, 2009). RWC is a measure of relative change in cell volume; ψ is the result of cell turgor and π , and thus depends both on solute concentration and cell wall rigidity and does not relate directly to cell volume (Kaiser, 1987; Jones, 2007). OA together with cell wall rigidity regulate turgor under dehydration, where the former is generally more effective and prevalent than the latter (Bartlett et al., 2012). Small cells are generally more conducive to OA than large ones. It is recognized that turgor, G_s and growth can be regulated by hydraulic and/or hormonal signals, directly or indirectly (Blum, 2016).

Plant Strategies to Mitigate Damage from Dehydration

From an agricultural perspective, drought is ultimately defined in terms of its effects on yield, since this is the relevant issue when addressing the improvement of crop production under water-limited environments (Passioura, 2007). Most plants that are grown in field conditions experience water stress during part of their growing cycle, especially at midday and early afternoon in the summer or due to the scarcity or absence of rain for long periods of time. This threat affects phenology, carbon fixation, distribution of assimilates and plant reproduction (Fuad-Hassan et al., 2008); for example, legumes are highly sensitive to water deficit especially during the reproductive period, flowering and pod filling (Araújo et al., 2015). Consequently, the timing of water deficits during the season (e.g. sowing, crop establishment,

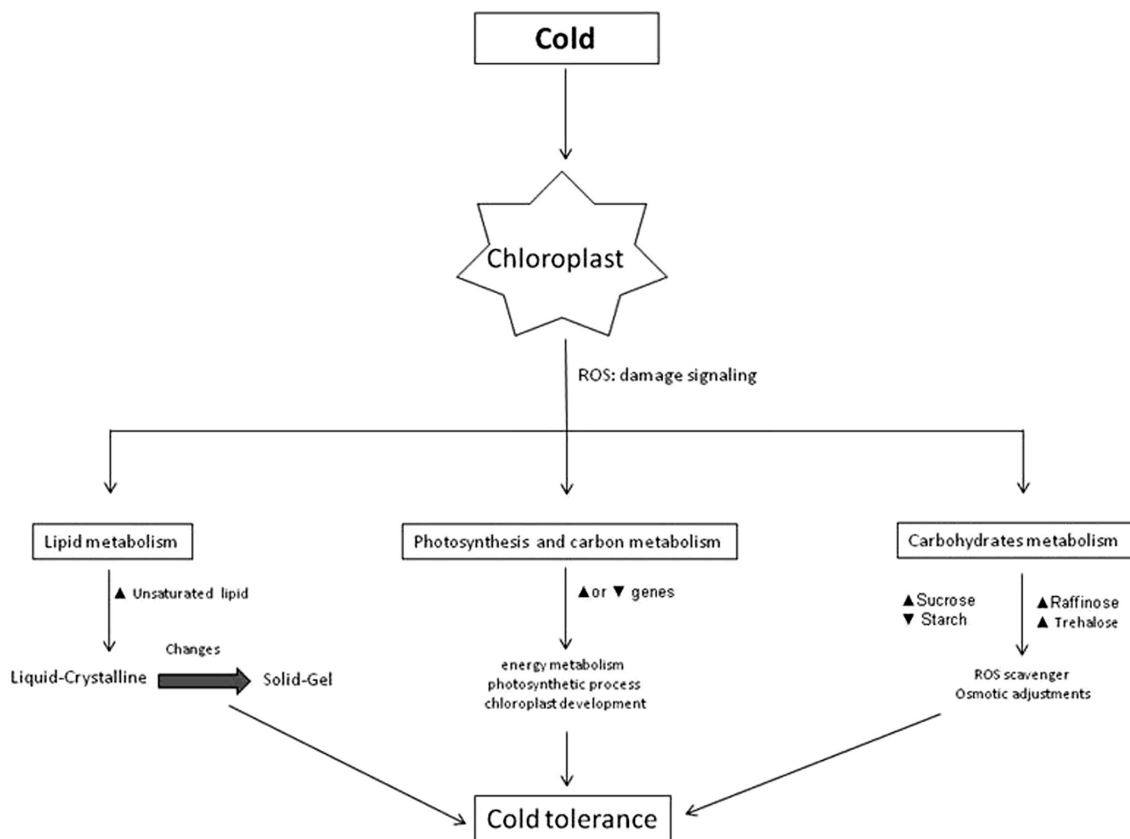


FIGURE 1.1 Schematic representation of how metabolic routes vary in response to cold.

flowering or grain filling) may have a much larger impact on yield than the intensity of drought per se (Pinheiro and Chaves, 2010). In this way, to maintain productivity, agriculture uses about 70% of water resources in the world. It is estimated that, by 2030, the requirement for irrigation will increase by 14% (FAO, 2009).

Mesophyte species that experience water stress modify or adjust their cell metabolism to the new conditions imposed by stress. When the regulation is inadequate and the metabolism is not adjusted to maintain its functions, they trigger a series of harmful effects that can cause the death of the vegetable. Regulation is strongly influenced by species and environment. Metabolic changes involve biochemical, physiological and structural modifications (Passioura, 2007). With some exceptions, the lack of water of tissues below a critical level is accompanied by irreversible changes in the structure and finally, the death of the plant (Azcón-Bieto and Talón, 2008). In nature, plants can either be subjected to slowly developing water shortage (days, weeks or months) or face short-term water deficits (hours to days). In the case of slow water deficits, plants can either escape dehydration by shortening their life cycle or optimize their resource gain in the long term through acclimation responses. In some modern maize hybrids the anthesis-silking interval under drought has become shorter and selection has possibly led to an increase in the growth of spikelets (Bänziger and Cooper, 2001). In the case of rapid dehydration, plants react to minimizing water loss or exhibiting metabolic protection (induced or constitutive) against the damaging effects

of dehydration and co-developing oxidative stress (Chaves et al., 2003). Fast and slow desiccation can have totally different results in terms of physiological response or adaptation (McDonald and Davies, 1996), but the importance of time in shaping plant response may change dramatically according to genotype and environment (Chaves et al., 2003).

Plants can strengthen their response to a drought by avoiding tissue dehydration, maintaining the potential water as high as possible or by tolerating low tissue water potential using metabolic strategies. Although many genes are induced by water deficit, the molecular functions of all these are not known. In addition, the impact of a change in gene expression of a gene with a known function, such as an enzymatic function, on cellular homeostasis may not be exactly understood (Bray, 2007). Dehydration avoidance is associated with a variety of adaptive traits involving minimizing water loss and maximizing water uptake. Water loss is minimized by density or regulation stomatal (Bell et al., 2007), by reducing light absorbance or by decreasing leaf area due to less cell division and expansion rates in leaves. One of the earliest water-saving mechanisms, present in a great majority of plants, is reduced leaf growth (Aguirrezábal et al., 2006) or the earlier senescence of older leaves in the case of prolonged stress (Pinheiro and Chaves, 2010). This reduction in foliage dimension or lower stomata density leads to a decreased transpiration area (Quan et al., 2016). Water uptake is maximized by adjusting the growth pattern to increase growth of roots. This is the main resource to maximize water absorption. This response is mediated by hormones: abscisic acid (ABA), ethylene and their

interactions (Wilkinson and Davies, 2002). Changes in the root/shoot ratio as well as temporary accumulation of reserves in the stem occur in several species under water deficit (Chaves et al., 2003). As the key process of primary metabolism, photosynthesis plays a central role in plant performance under drought (Pinheiro and Chaves, 2010). The decline observed in leaf net carbon assimilation (A) as a result of plant water deficits is followed by an alteration and partitioning of the photo-assimilates at the whole plant level, corresponding in general to an increase in the root/shoot ratio (Sharp, 2002).

Experience from drought-resistant cereal cultivation during a century of scientific breeding clearly indicates that drought resistance in crop plants under stress is mainly derived from their ability to sustain tissue hydration during drought (i.e. dehydration avoidance), rather than an ability to sustain biological function when tissues are dehydrated (i.e. dehydration tolerance) (Araus et al., 2012).

Response Mechanisms That Take Place in Leaves

In order to avoid excessive water loss in times of drought, regulation of stomata aperture together with the reduction of the leaf area are the immediate responses of plants, which could result in a dehydration cell that would produce xylem cavitation, causing plant death (Comstok, 2002). However, a stomatal aperture is essential in leaf cooling by latent heat exchange, and this characteristic is an objective of selection in plant breeding (Lu et al., 1997). For example, many species have been classified as isohydric or anisohydric depending on the sensitivity of stomata to soil dehydration. Isohydric plants are those that close their stomata when they sense a drop in soil water potential or an increase in atmospheric demand. On the other hand, anisohydric plants continue to transpire even when soil water content diminishes, because these plants are keeping their stomata open longer (Tardieu and Simonneau, 1998). The different response of stomata to water scarcity is also associated with different root/shoot ratios, with the anisohydric stomatal behavior often being associated with larger root systems and high capacity for osmoregulation that supports water uptake until soil water content is low. Osmoregulation requires a dehydration signal to be developed, more likely to take place in aniso- than in isohydric plants. The anisohydric strategy allows a closer match between water availability and consumption, with a positive impact on season growth (Chaves et al., 2016). Regardless of the mechanism of perception and signaling that causes stomatal closure, many plants show a tendency to increase water use efficiency (WUE) when the stress is moderate as a result of a non-linear relationship between carbon assimilation and G_s , by which the plant restricts the loss of water without excessively affecting photosynthesis (Blum, 2005; Taiz and Zeiger, 2003). When comparing C_3 and C_4 species it is apparent that C_4 plants exhibit higher WUE (A/E ratio) due to higher A and lower transpiration (E). In warm regions, where C_4 species evolved, photorespiration is stimulated considerably, as well as the demand for transpiration for cooling. By increasing CO_2 around the carboxylating enzyme Rubisco (RuBP), C_4 plants greatly enhanced carboxylation efficiency and were able to inhibit photorespiration (Sage, 2004). By producing smaller stomata density or reducing stomata aperture plants will function at low stomata conductance (G_s) and have lower E (Chaves et al., 2016).

However, in this case, the CO_2 concentration at the RuBP site in the mesophyll cells is limited (Perdomo et al., 2017). In this sense, Perdomo et al. (2017) observed that the limitations to photosynthesis under drought were mainly caused by a stomata closure (lower G_s) and increased leaf resistance to CO_2 transport from the atmosphere to the site of carboxylation (diffusive limitations) in C_3 and C_4 species. Conversely, under the combination of water deficit and heat stress, biochemical limitations have been observed with decreased RuBP activation and impaired ATP synthesis, which is due to a decrease in electron transport. Experimental studies on CO_2 assimilation of mesophytic C_3 plants under water stress revealed a decreased relative water content (RWC), actual rate of A and potential rate (A_{pot}). In this way, there are two general types of relation of A_{pot} to RWC, which are called Type 1 and Type 2. Type 1 has two main phases. As RWC decreases from 100% to 75%, A_{pot} is unaffected, but decreasing G_s results in smaller A , and lower CO_2 concentration inside the leaf (C_i) and in the chloroplast (C_c), the latter falling possibly to the compensation point. Below 75% RWC, there is metabolic inhibition of A_{pot} , inhibition of A then being partly reversible by elevated CO_2 ; G_s regulates A progressively less, and C_i and CO_2 compensation points rise. In the Type 2 response, A_{pot} decreases progressively at RWC 100% to 75%, with A being progressively less restored to the unstressed value by elevated CO_2 . Decreased G_s leads to a lower C_i and C_c but they probably do not reach compensation point: G_s becomes progressively less important and metabolic limitations more important as RWC falls (Lawlor and Cornic, 2002). The primary effect of low RWC on A_{pot} is most probably caused by limited RuBP synthesis, RuBP activity or activation state, as a result of decreased ATP synthesis, either through inhibition of coupling factor activity or amount due to increased ion concentration or impaired activation of RuBP by Rubisco activase (Perdomo et al., 2017). Electron transport is maintained (but down-regulated) over a wide range of RWC (Sage et al., 2008; Taylor et al., 2011). Metabolic imbalance results in amino acid accumulation and decreased protein synthesis. These conditions profoundly affect cell functions and ultimately cause an excess of radiant energy that is not used for photosynthesis and that the plant must eliminate in order to avoid the overproduction of reactive chemical species that potentially can produce oxidative damages that would compromise the photosynthetic (Chaves et al., 2003). Autotrophic organisms have direct and indirect mechanisms that capture the excess of incident photons (photoreceptors, photochromes, neochromes, phytochromes, rhodopses and cryptochromes), variation of pH in the thylakoid lumen, changes in the oxidation-reduction state, production of reactive oxygen species (ROS) and accumulation of metabolites, which will induce changes in nuclear gene expression and gene expression in the plastid. These mechanisms attempt to decrease the damage caused by the adverse situation (Li et al., 2009). In order to avoid excess light, plants can reduce light absorbance by leaf rolling, a dense trichome layer increasing reflectance and steep leaf angles. They can divert absorbed light by photochemical reactions to other processes such as thermal dissipation (Pastenes et al., 2004; Baker, 2008). In fact, it is widely accepted that photosynthesis regulation in response to the environment is highly dynamic and is modulated in the short term by thermal energy dissipation. This increase in energy dissipation is linked (at least partially) to a parallel increase in photoprotective carotenoid levels. In this way, the

“xanthophyll cycle” plays a primordial role in the thermal dissipation process, which consists of light-dependent interconversion of three xanthophylls (oxygenated carotenoids): violaxanthin, antheraxanthin and zeaxanthin. This is a cyclic reaction involving a de-epoxidation sequence of violaxanthin di-epoxide via antheroxanthine mono-epoxide to form zeaxanthin (without epoxy groups). The cycle is regulated by light; violaxanthin is de-epoxidated to antheraxanthin and zeaxanthin under conditions of high photon flux (or when photosynthetic activity is diminished by stress), while in the dark (or when the stress factor is absent), zeaxanthin is again epoxidized to violaxanthin (Demming-Adams and Adams, 1996; Nelson and Yocum, 2006). Moreover, other processes have significant photoprotective and stabilizing functions, including the antioxidant properties of vitamin E (α -tocopherol), a constitutive component of the lipid matrix of thylakoid membranes (Li et al., 2009). In species under water deficit, the use of absorbed light (photosynthesis or photorespiration) and thermal dissipation is not sufficient to retain excess energy; electrons in a highly excited state are transferred to molecular oxygen (O_2) that form the reactive oxygen species (ROS), such as H_2O_2 , O_2^- , HO^- and 1O_2 . All these molecules are highly toxic and can cause oxidative damage to proteins, DNA and lipids (Miller et al., 2010). In this situation, the plant has antioxidant molecules and enzymes that are in different cell compartments and can scavenge ROS (superoxide dismutase, catalases, ascorbate-glutathione cycle such as glutathione reductase and ascorbate peroxidases). The antioxidant activity depends on the degree of severity of stress, genotype and stage of development. The acclimatization of plants to drought is associated with increased activity of antioxidant enzymes that maintain the concentration of ROS at relatively low levels (Signorelli et al., 2013; Quan et al., 2016). On the other hand, seedlings subjected to water deficit show nitric oxide (NO) production (Arasimowicz-Jelonek et al., 2009). However, when there is a deregulated synthesis or overproduction of NO that may have toxic physiological consequences, it results in nitrosative stress due to reactive nitrogen species (RNS) formation. RNS are formed by the interaction of NO with free radicals and oxygen. RNS include NO^- , nitrogen dioxide (NO_2^-), S-nitrosothiols (SNOs) and peroxynitrite ($ONOO^-$) (Airaki et al., 2011). Water stress in *Lotus japonicus* results in an increase in NO levels and reduced S-nitrosoglutathione reductase activity (an enzyme that maintains low levels of RNS), especially in roots (Signorelli et al., 2013). Under environmental stress, an increase in ROS and RNS levels can cause damage in cells, but it must be pointed out that both ROS and RNS can also serve as secondary messengers in signaling for the activation of defense responses to pathogens, abiotic stress, programmed cell death and development (Suzuki and Mittler, 2006; Arasimowicz-Jelonek et al., 2009; Gill and Tuteja, 2010; Miller et al., 2010; Airaki et al., 2011; Signorelli et al., 2013).

Response Mechanisms That Take Place in Roots

Root systems are responsible for water and nutrient uptake and provide physical stability, and store nutrients and carbohydrates. In addition, roots may act as sensors for water deficit conditions and send signals to shoots above ground. It is well documented that species adapted to dry climatic regimes generally have higher root/shoot ratios and deeper root systems than species that

are suited to humid climatic conditions (Brunner et al., 2015). Although the root/shoot ratio tends to increase, the biomass of fine roots in particular is often reduced as a consequence of reduced transpiration and respiration rates. The benefit, however, is that young roots are able to take up water more efficiently than older ones, and thus, root shedding and re-growth represent a more suitable acclimation of plants to reduced water supply if the plant can afford this strategy. In experiments with trees it was observed that whether a tree maintains old roots or sheds old roots and produces new ones in response to drought is determined by the benefit to cost ratio in terms of water uptake and carbon expenditure. Root shedding and the construction of new roots mean the investment of a considerable amount of energy in the process of root turnover (Eissenstat et al., 2000). Before this, plants cease growth and close the stomata to prevent water loss under drought conditions, which results in a simultaneous decrease in photosynthesis. However, maintenance respiration responds more slowly to drought than photosynthesis, resulting in a carbon deficit and forcing the plant to utilize stored carbohydrates. If the carbon deficit persists for a long time, carbohydrates will be depleted and plants will experience carbon starvation, resulting in plant mortality. In the roots of *Robinia*, Yan et al. (2017) observed an increase in soluble sugar but a decrease in starch, indicating that the roots began to utilize the starch, creating a carbon deficit in the roots. Regier et al. (2009) applied drought conditions to two contrasting *Populus nigra* clones and observed that the drought-adapted clone had significantly more starch but significantly less sucrose, glucose and fructose in the roots and conversely a drought-sensitive clone had a reduction of carbohydrate due to lower starch levels inducing degradation of starch to maintain root respiration. In soybean, under severe water deficit, there was an increase in transcripts associated with starch synthesis and a decrease in transcripts associated with starch degradation. Conversely, galactinol and raffinose synthase related genes were up-regulated, which might enhance osmotic tolerance in the root (Song et al., 2016b). In this way, the elevated level of proline found in alfalfa roots indicates the ability to regulate water deficit stress tolerance (Rahman et al., 2016). Generally, a decrease in soluble sugars is observed in the branch, stem, bark and root tissues after rewatering due to recovery of tissue growth (Brunner et al., 2015; Yan et al., 2017).

Summary

Cold, drought and salinity are those environmental factors which affect plants in many respects and which, due to their widespread occurrence, cause the most fatal economic losses in agriculture. All three forms of abiotic stress affect the water relations of a plant on the cellular as well as whole plant level, causing specific as well as unspecific damage (Figure 1.2) and responses. The plant's response to these stresses (drought, salt and cold) is through the response mechanisms that are raised at both molecular and cellular levels, as well as physiological and biochemical, which allow them to acclimate and survive stress. In general, the first step in switching on a molecular response in response to an environmental signal is its perception by specific receptors; these are physical signals (changes in the pressure of cell turgor, alterations in the walls and cellular volume) that are then converted to biochemical

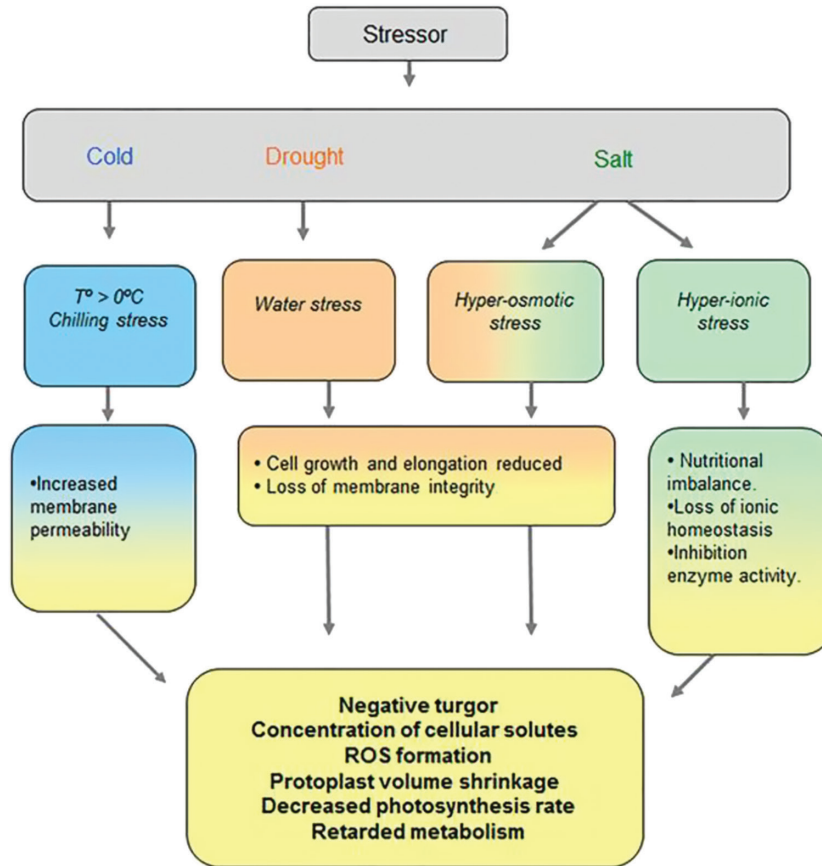


FIGURE 1.2 Similar (bold types) and dissimilar damages produced by cold, salt and drought in plant tissues.

signals, which are generated in response to stress (Bray, 2007). These include receptor-like kinases, receptor tyrosine kinases, G-protein coupled receptors, ionotropic channel related receptors, histidine kinases, nuclear hormone receptors and extra- and intracellular Ca^{2+} sensors. Ca^{2+} influx and histidine kinases have been identified in response to cold. It has been suggested that in *Arabidopsis* a heterotrimeric G-protein is involved in ABA response in guard cells (Xiong and Ishitani, 2006). Then, followed by the generation of secondary messengers (inositol phosphates, ROS) that can modulate the intracellular Ca^{2+} level and initiate a signal transduction cascade that involves protein phosphorylation/dephosphorylation, where different Ca^{2+} sensors are included, a protein decodes their signals and has a Ca^{2+} binding motif, the so-called EF hand motif: calmodulins (CaMs), calcineurin B-like proteins (CBLs), Ca^{2+} -dependent protein kinases (CDPKs), mitogen-activated protein kinase (MAPKs) and phospholipid-cleaving enzymes (Shi, 2007). In salt stress, it is important to emphasize the ion-specific signaling pathway SOS (salt overlay sensitive), which responds to changes of Ca^{2+} levels in cytoplasm, described in *A. thaliana* (Zhou et al., 2007). Finally, these would reach a large number of genes, enzymes, hormones, and metabolites. The products of these genes can participate in the generation of regulatory molecules such as ABA, and ethylene and salicylic acid, which in turn can initiate a secondary signaling process (Xiong et al., 2002). The different environmental variables that determine osmotic stress constitute a complex of stimuli that possess different and sometimes related attributes in

which each one of them provides particular information to the cells. Given this multiplicity of signals, it is expected that the plant possesses multiple primary sensors that perceive the signal of stress. The increase of Ca^{2+} in cytoplasm, as a result of the influx from apoplast or the release of intracellular compartments, is an early response to osmotic stress (Shi, 2007). The products of inducible genes to osmotic stress can be classified into two groups: the first group includes functional proteins (which participate directly in the biochemical mechanisms of damage control, repair and acclimatization: aquaporins and some key enzymes of osmolytes biosynthesis, chaperones, antioxidants), whereas the second group comprises regulatory proteins involved in signal transduction and gene expression (e.g. transcription factors, protein kinases, protein phosphatases) as well as diverse effectors involved in signaling (e.g. calmodulin-binding protein, SOS pathways; Seki et al., 2003). Hundreds of genes are induced or repressed under osmotic stress. Many of these stress-inducible genes are activated by ABA, and their products may improve tolerance to stress (Xiong, 2007). It is not surprising that gene expression is regulated by this phytohormone, although not all genes that are induced by stress are regulated by ABA, indicating the existence of several signaling pathways (Ishitani et al., 1997). Among the most important pathways are ABA-dependent and ABA-independent, which isolate and characterize the *cis*-regulatory elements and the transcriptional factors responsible for its activation (Busk and Pages, 1998). The ABA-regulated promoters, called ABRE (ABA response elements), contain ACGT

TABLE 1.1

Promoters, *Cis*-Regulatory Elements and Transcription Factors in Response to Osmotic Stress

Promoters	<i>Cis</i> Elements	Transcription Factors	Stressor
RD29A	ABRE	CBF/DREB1	Cold
RD29A	DRE/CRT	DREB2	Salt, ABA and drought
RD29B	ABRE	bZIP	Salt and drought
RD22	MYB/MYC	MYBR/MYCR	Drought and ABA

nucleotides as the *core* of their sequence and form part of the elements called G-box. More than 20 ABREs have been described in genes that respond to dehydration and drought, which bind to trans- factors regulated by ABA, such as bZIP (Kobayashi et al., 2008). Also, other ABA-responsive transcription factors known as MYBR/MYCR constitute an indirect pathway for ABA regulation through the R22 promoter gene. On the other hand, ABA-independent genes are characterized by containing a conserved dehydration response element (DRE, TACCGACAT) in their promoter region, related to gene regulation by interaction with an ABA-independent signaling cascade and matched by the gene RD29B promoter. It is a faster response route than the previous one (Table 1.1). This was discovered through studies of the RD29A promoter gene, which is induced by both ABA-dependent and independent pathways (Xiong et al., 2002; Shinozaki and Yamaguchi-Shinozaki, 2007). The genes that are upregulated by ABA (a) encode enzymes that function in the biosynthesis

of compatible solutes that could lower leaf water potential and facilitate water uptake and retention, (b) can directly detoxify ROS (Jiang and Zhang, 2002) and (c) encode polypeptides that may help to restore the native structure of abnormally folded proteins or could promote the degradation of unfolded proteins that cannot be repaired (Xiong et al., 2007). Although osmotic stress alone can activate these stress-responsive genes, ABA can synergistically enhance their expression, enhancing the ability of the plants to respond to stress (Tuteja et al., 2011). In addition, a complex network of response involving ABA and PAs and/or nitric oxide (Arasimowicz-Jelonek et al., 2009) has been identified and observed in different species, such as *Lotus tenuis* (Espasandin et al., 2018), *Coffea canephora* (Marracini et al., 2012) and *Lycopersicon esculentum* (Diao et al., 2017) exposed to salt, water and cold stress, respectively. Finally, the vegetal metabolism is altered, inducing biochemical and physiological responses that create tolerance (Figure 1.3).

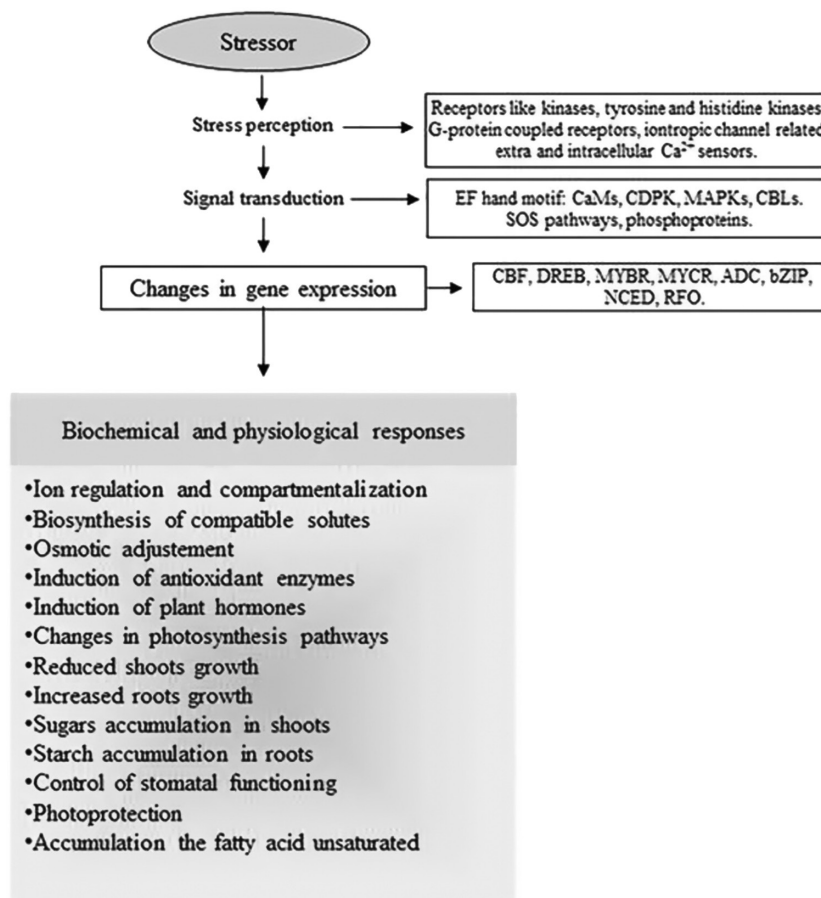


FIGURE 1.3 Biochemical and physiological responses to drought, salt and cold stress in plants.

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Recent Advances on the Modulatory Role of ATPases toward Salt Tolerance in Plants

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