Parvaiz Ahmad · M.M. Azooz
M.N.V. Prasad *Editors*

Salt Stress in Plants

Signalling, Omics and Adaptations

Springer

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Preface

Anthropogenic pressures are implicated in the degradation of invaluable natural resources. Assessing the impacts of global soil salinization on plant growth and productivity and identifying approaches for mitigation salinization are subjects of global importance. It is reported that about 7% of the total land on Earth and 20% of the total arable area are affected by a high salt content. Plant productivity is also affected by the elevated levels of salt content in the soil. The reason for the low production is that various metabolic processes that work independently or in coordination with one another are affected by the deleterious effects of salt.

Poly-omics – namely, proteomics, genomics, micromics, transcriptomics, metablomics, inomics, metallomics, etc. – have emerged as a powerful tool for understanding the mechanism of plant response toward salinity stress. The exploitation of different genes and proteins involved in the regulation of various environmental stresses will be very useful in generating crops with enhanced food production under salinity stress. With the help of metabolomics, we will recognize different metabolic pathways the plant is rearranging during stress. Plants perceive both external and internal signals and use them to regulate various responses for their development.

During salinity stress, plants respond in various ways and can withstand the stress. Salinity stress is responsible for osmotic, ionic, and oxidative stresses, which lead to reduced growth and development of the plant. Plants can tolerate these stresses by the accumulation of osmolytes and osmoprotectants. Another machinery is the expression of different types of enzymatic and non-enzymatic antioxidants. Understanding the full mechanism of salt tolerance through different means is an enigmatic subject for scientists in general and plant biologists in particular.

The outline of this volume, "*Salt Stress in Plants: Omics, Signaling and Adaptations*," encompasses the following: Chapter 1 deals with advances of metabolomics to reveal plant response during salt stress. Chapter 2 narrates the role of microRNAs (micromics) in response to salt stress in plants. Chapter 3 sheds light on the role of proteomics in salt-stressed plants. Chapter 4 discusses improving salinity tolerance in plants through genetic approaches. Chapter 5 describes the role of LEA

proteins in salinity tolerance in plants. Chapter 6 highlights the effect the salt stress on crop production and the role of omics in salinity tolerance. Chapters 7, 8 and 9 deal with the role of different kinds of signaling molecules in plants under salt stress. Chapters 10 and 11 examine the approaches to improve salt tolerance in rice and maize. Chapter 12 highlights the role of phytochromes in stress tolerance. Chapter 13 discusses alleviating salinity stress through arbuscular mycorrhiza. Chapter 14 deals with breeding approaches in stress tolerance in citrus. Chapter 15 highlights the effect of salt stress in photosynthesis under ambient and elevated atmospheric CO_2 concentrations. Chapter 16 deals with nitrogen-use-efficiency in plants under salt stress. Chapter 17 sheds light on the response of salt-affected plants to cadmium, and Chap. 18 highlights the role of plant tissue culture in screening the salt tolerance in plants.

This volume will provide valuable information about the omic approaches, signaling, and responses of plants under salt stress. We would like to thank all the authors of this volume for their contributions. We are also thankful to my colleagues who helped us directly or indirectly in completing this volume. We are also grateful to Hanna Smith (Associate Editor, Springer) and Margaret Burns (Developmental Editor, Springer) for their help, suggestions, and timely publication of the volume.

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Hyderabad, India   M.N.V. Prasad

Contents

Brief Biodata of Editor and Co-editors

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Dr. Parvaiz Ahmad is an assistant professor in botany at A.S. College, Srinagar, Jammu and Kashmir, India. He completed his postgraduation in botany in 2000 from Jamia Hamdard, New Delhi, India. After receiving a doctorate degree from the Indian Institute of Technology (IIT) Delhi, India, he joined the International Centre for Genetic Engineering and Biotechnology, New Delhi, in 2007. His main research areas are stress physiology and molecular biology. He has published more than 30 research papers in peer-reviewed journals and 16 book chapters. He is also the editor of four book volumes (three with Springer Science + Business Media, NY, and one with Studium Press Pvt. India Ltd., New Delhi, India). He is the recipient of the Junior Research Fellowship and Senior Research Fellowship conducted by CSIR, New Delhi, India. Dr. Ahmad has been awarded the Young Scientist Award under Fast Track scheme, in 2007, by the Department of Science and Technology, Government of India, New Delhi, India. He is actively engaged in studying the molecular and physio-biochemical responses of different agricultural and horticultural plants under environmental stress.

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Professor M.M. Azooz is a professor of plant physiology at the Department of Botany, Faculty of Science, South Valley University, Qena, Egypt. He received his B.Sc. in 1984 and M.Sc. in 1990 from Assiut University, Egypt. He received his Ph.D. in 1997 from Tübingen University, Germany. He has published more than 70 research articles in peer-reviewed journals and five book chapters. He has supervised many M.Sc. students and five Ph.D. scholars. He is an editorial board member and reviewer of many international journals. Professor Azooz has been included in *Marquis Who's in the World* (Biography, 28th Edition, 2011), and in the "Top 100 Scientists" list, International Biographical Centre, Cambridge,

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Professor M.N.V. Prasad is a professor at the Department of Plant Sciences at the University of Hyderabad, India. He received his B.Sc. (1973) and M.Sc. (1975) degrees from Andhra University, India, and his Ph.D. degree (1979) in botany from the University of Lucknow, India. Prasad had published 141 articles in peer-reviewed journals and 84 book chapters and conference proceedings in the area of environmental botany and heavy metal stress in plants. He is the author and editor for 15 books (John Wiley and Sons Inc. New York; CRC Press, Boca Raton; Springer-Verlag, Heidelberg; Narosa Publishing House, New Delhi; Kluwer Academic Publishers, Dordrecht; Marcel Dekker, New York; Fizmatlit Publishers, Moscow; and Ministry of Environment and Forests, Govt. of India). He is the recipient of the Pitamber Plant National Environment Fellowship of 2007, awarded by the Ministry of Environment and Forests, Government of India. He has served as a visiting professor and guest researcher in many universities in different parts of the world, including Australia, Belgium, Canada, Finland, Kazakhstan, Poland, Portugal, and Sweden.

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Chapter 1
Recent Advances of Metabolomics to Reveal Plant Response During Salt Stress

Ruby Chandna, M.M. Azooz, and Parvaiz Ahmad

Abstract Salt stress is the major limiting factor in agriculture and portraits a major challenge to food security. The adverse effect of salt stress is expressed on whole plant levels. Plants have acquired various processes that functions to balance cellular hyperosmolarity and ion disequilibrium in an effort to combat salt stress. These processes occur due to significant changes in the gene expression that in turn bring about changes in plant metabolism. These metabolic changes help the plant to adapt to disorganized metabolic homeostasis. It has been observed that adverse growth conditions have impact on the synthesis of secondary plant products or metabolites that help in plant defence. The diverse nature of these metabolites has lead to the development of 'Metabolomics'. The metabolite fingerprinting and profiling approaches provides accurate identification and quantification of stressed sample even before they can bring about change(s) in the transcriptome or proteome. Using metabolic profile changes as a marker for stress physiology, metabolic movements and factors can be analysed in combination with other 'omic' techniques, such as transcriptomics. Revealed analyses of salt acclimation effects and related stress factors to salinity stress may provide help in crop breeding programs to develop

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salt tolerance varieties. In this review, we will focus on recent advancements and application of metabolomics in plants under salinity stress.

Keywords Salinity • Signaling • Phenolic compounds • Alkaloids

Salinity in agriculture has been a major restricting factor in food production. Soil salinity is known to restrict the land use and limits crop yield. The various environmental programs carried throughout the world estimates that approximately 20% of agricultural land and 50% of cropland in the world is salt-stressed (Munns and Tester 2008). Hence, the existing soil salinity is a large confront for food security. Increase in levels of water-soluble salts e.g. NaCl, Na_2CO_3 and $CaCl_2$ is mainly due to irrigation, results in soil salinity. Soil salinity results in reduced biomass production by affecting important physiological and biochemical processes of plant (Ahmad and John 2005; Ahmad and Sharma 2006, 2008, 2010; Ahmad 2010; Ahmad et al. 2010a, b, c, 2012).

The adverse effect of salt stress is expressed on whole plant level, and appears during all developmental stages including germination, seedling and vegetative stages. However, tolerance in respect to salt stress varies at different plant developmental stages and also from species to species. Salt stress occur as a calamitous episode, be imposed constantly or from time to time and then gradually becoming more severe at any stage during development. The plant respond to salt stress by various processes that functions in coordination to balance cellular hyperosmolarity and ion disequilibrium. Salt tolerance in plants and their yield stability are complex genetic traits that are complicated and difficult to establish in crops.

Plant's ability to tolerate salt is dependent on multiple biochemical pathways that lead to production of osmotically dynamic metabolites, free radicals and specific proteins to manage ion and water flux. Thus providing support to scavenging oxygen radicals and in turn maintaining ion homeostasis. Therefore there was need to determine the underlying biochemical mechanisms of salinity tolerance so as to provide plant breeders with appropriate indicators. But salt stress has showed to affect many intracellular substances, like nucleic acids, proteins, carbohydrates and amino acids (Ahmad and Sharma 2008, 2010; Ahmad et al. 2010a, b, c; Ahmad 2010). Thereby the introducing molecular biological techniques into plant stress physiology provided an enhanced effort that lead to the identification of stress-inducible genes (Bartels and Sunkar 2005; Umezawa et al. 2006). These studies succeeded in over-expression of genes that are known to be involved in stress responses, provided tolerance to abiotic stress. Another approach, quantitative trait locus (QTL) analysis brought about benefits in the enabled creation of stress-tolerant crops by combining QTLs for various stress tolerances traits (Takeda and Matsuoka 2008; Krasensky and Jonak 2012). Several studies related to QTL in various salt stress tolerances have been reported. For example, Ren et al. (2005) identified the SKC1 locus encoding a high affinity K^+ transporter (HKT)-type sodium transporter by analyzing a QTL for salinity tolerance using salt-tolerant and salt-susceptible rice varieties.

However, plant responses to salinity involve diversified changes in the activity of genes and proteins, which invariably lead to changes in plant metabolism. It is now known that plants have numerous metabolic pathways that direct to thousands of secondary products which are capable of effectively responding to salt stress situations. These pathways, often diverge from primary metabolic pathways upon initial gene duplication (Nascimento and Fett 2010; Mastrobuoni et al. 2012). So, the different type of growth conditions has a noteworthy impact on the synthesis and accretion of secondary plant products. Because of these extremely assorted chemical natures of metabolites, metabolome analyses can provide accurate identification and quantification from a single stressed sample (Birkemeyer et al. 2005). More precisely, the metabolite fingerprinting approach and its summary provides identification of the early compounds that signal the perception of stress even before they can bring about change(s) in the transcriptome or proteome could be detected to access the eventual biological information current connecting gene expression and metabolic phenotype. In this review, we will be summarizing some of the plant stress physiology and techniques used to study the metabolome of plants during salt stress.

Physiology of Plants Under Salt Stress

Mechanisms of plants towards salt tolerance occur by restricting the entry of salt into the plant (especially minimizing the accumulation of salt in photosynthetic tissues and cytoplasm) (Munns 2002). The plant follows two major adaptive strategies towards high environment salinity tolerance: firstly to avoid stress due to different physical and physiological barriers, secondly enhancing the adaptive mechanisms internally that will enable successful survival. Therefore, the Na^+ uptake and its transport regulation across the plasma membranes and tonoplast is one of the key factors that establish the plant cell response to salinity stress (Dajic 2006). Avoidance of salt uptake can take place by salt exclusion; it is a very efficient but complex way of reducing the permeability of massive ion in the root zone, especially sodium. This process enables a low uptake and accumulation of salts in the upper parts, especially in the transpiring organs of the plant. Many glycophytes are known to show better skills for Na^+ exclusion from the shoot and also for maintaining elevated levels of K^+ (Flowers and Hajibagheri 2001). Studies have revealed salt in-tolerant plants, such as beans and maize are known to be the most outstanding Na^+ excluders (Bayuelo-Jimenez et al. 2003) whereas salt tolerant crops like bread wheat has reduced speed of Na^+ transport to the shoots and high K^+/Na^+ intolerance (Gorham 1990).

A study done by Munns et al. (1988) and Jeschke and Hartung (2000) have shown salt exclusion to function at the cellular as well as at the whole plant level and to a greater extent is related to regulation of K/Na ion selection. In mangrove *Avicennia marina* is known to have 98% degree of salt exclusion property (Ball 1988). Whereas it was demonstrated by Munns et al. (1999) glycophyte or halophyte, has the property of restraining of Na^+ uptake and accumulation in the shoots. In some salt tolerant

species, for example wheat have the property to exclude salts is achieved by changing sodium and calcium ions, rather than bringing about modification in osmotic potential, as adsorption on membranes of root cells of calcium ions directs towards reduced penetration of monovalent cations (Munns et al. 1999).

Salt excretion is another very efficient way of preventing excessive absorption and building up of salts in photosynthetic tissues. This mechanism is equipped with developed special features, which are mostly present in leaf epidermis, known as salt glands and salt hairs (bladders). These structures are commonly found in many halophytes such as *Spartina*, *Aeluropus* (Poaceae), *Limonium*, *Armeria* (Plumbaginaceae), *Atriplex* (Chenopodiaceae), *Glaux* (Primulaceae), *Tamarix*, *Reamuria* (Tamaricaceae), and in mangrove species, e.g. *Avicennia*, *Aegiceras* and *Acanthus* (Popp 1995). The glandular structures that are involved in salt excretion may vary in structure, position, mechanism and also in ecological significance. The simplest ones are two celled found in *Spartina* and *Aeluropus,* and three-celled types known to occur in *Chloris gayana*. There are also complex structures composed of 5–9 cells in *Avicennia*, 8 cells present in *Tamarix* and also 16 celled present in the family Plumbaginaceae (Crawford 1989). Glandular structures are present all over the surface area of the shoot, and are most abundant on the leaves.

Still excessive exposure of plants to salt stress can lead to the production of reactive oxygen species (ROS) such as H_2O_2 (hydrogen peroxide), $O_2^{\cdot-}$ (superoxide), $^1O_2$ (singlet oxygen) and $^{\cdot}OH$ (hydroxyl radical). Excess ROS is a source of toxic reactions like lipid peroxidation, protein degradation and DNA mutation (Vinocur and Altman 2005; Pitzschke et al. 2006; Ahmad et al. 2008, 2009, 2010b, 2011, 2012). In plant cells, H_2O_2, superoxide anion (O_2^-), and hydroxyl radical ($^{\cdot}OH$) are generated due to oxidative damage to cells during environmental stress in the cytosol, chloroplasts, mitochondria, and the apoplastic space and they have the potential to cause (Mittler 2002). Research work has revealed that ROS has an important role as signal transduction molecules in plants. It is involved in mediating responses to environmental stresses, pathogen infection, and programmed cell death (Torres and Dangl 2005). Increased production of ROS related to salt stress causes membrane injury (Shalata et al. 2001). This increase in levels of ROS results from closure of stomata that leads to reduced in CO_2 concentration within the chloroplasts and also decreases in $NADP^+$ concentration causing photoinhibition (Foyer and Noctor 2003).

Among all these synchronized physiological responses in plants, abscisic acid (ABA), the plant hormone, plays a essential role. ABA is a stress hormone as for its rapid accretion towards the response to stress and its intervention, help plant endurance over much stress. The first requirement is that ABA production should be rapidly triggered by the stress signals so that inhibition of physiological functions is avoided. Secondly, ABA should be quickly degraded and deactivated once the stress is reassured so that normal plant growth and functions can recommence.

Research on plant tolerance towards salt stress cover many portions of its influence on plant behaviour, which includes alterations at the morphological, physiological and molecular levels. Previously, stress studies are focused on: transgenic plants development, improvement of plant breeding and modification in the genetic structures of existing crops towards enhanced adaptation to salinity conditions.

Recently, the progress of research in 'omics' like proteomics and metablomics and has created a better platform for understanding of molecular mechanism in salinity stress (Tester and Davenport 2003).

Cell Signalling and Secondary Signal Molecules During Salt Stress

During environmental stress plant cells receive stress signals that are influenced by various signalling pathways. The secondary messengers, stress responsive plant hormones, signal transducers and regulatory transcriptional molecules together to induce signals via signalling pathway. Early response in plant cells towards salinity stress is Ca^{2+}, derived; leading to a sudden increase in its concentration in cytosol either from influx of Ca^{2+} from the apoplastic space or release from internal stores. The release of Ca^{2+} is further controlled by second messengers for example, cyclic ADP ribose, $NADP^+$ and inositol polyphosphates and that are present as ligand-sensitive Ca ion channels. These molecules enable the release of Ca^{2+} in plant cells particularly in guard cells (Schroeder et al. 2001). Hrabak et al. (2003) reported that two protein kinases are assumed to be the targets of the Ca^{2+} signal in plants. One is SnRK3-type kinases, whose action is reliant on the Ca^{2+}-binding calcineurin B-like (CBL) proteins (Krasensky and Jonak 2012; Sarwat et al. 2012). Work done by Luan (2009) in Arabidopsis has showed SnRK3 as one of the best characterized protein kinase which was eventually recognized as a vital factor in salt stress response. The other protein kinase concerned in stress response is Ca^{2+}-dependent kinase (CDPK).

Mitogen activated protein kinase (MAPK) mechanism in plant cell are as well accountable for the assembly of osmolytes and antioxidants. Receptors/sensors such as kinases (histidine kinases and protein tyrosine kinases) and G-protein are known to activate these MAPK pathways (Kong et al. 2011; Zhang et al. 2011).

Late embryogenesis–abundant (*LEA*)-type genes and the dehydration-responsive element (DRE)/C-repeat (CRT) among the class of important responsive genes towards stress play role in regulation of osmolyte production. Researchers showed that *LEA* -type genes represents damage repair pathways (Xiong and Zhu 2002). Since the activity of phospholipase C in plants that is regulated by G-proteins, and phosphoinositols organize the up-regulation of these *LEA* – like genes under salt stress. G-protein–related receptors may also provide with membrane-bound receptors for ABA response (Wang et al. 2001). Under salinity stress, ABA plays a very important role in bringing about a radical change in the expression profile of gene and cellular processes of plant (Park et al. 2009). Other plant hormones play direct or indirect substantial task during abiotic stress. ABA during abiotic stress is known to interconnect with Salicylic acid (SA), ethylene (ET) as well as jasmonic acid (JA) (Grant and Jones 2009).

Plasma membrane plays a role of barrier between living cells and the surrounding environments. It also has an important part in the insight and conduction of exterior details. Variation in phospholipid components occurs when osmotic stress

is initiated and this change is detected in plants (Munnik et al. 1998). However, the major role of phospholipids is they form the backbone of cellular membranes and serve as precursor for the production of second-messenger molecules. The relevant enzymes involved in cleaving are the phospholipases (PIP) A2, C, and D. PIP besides being involved in signal transduction is also involved in several processes, like employing, assembly and transportation of signalling complexes to the specific membrane locations (Martin 1998). PIP 2 is also involved in cellular ion homeostasis. *PI5K*, is one of the gene that encodes a phosphatidylinositol 4-phosphate 5-kinase (PIPK) that functions in the production of PIP 2 (Mikami et al. 1998). As osmotic stress increases, so does the production of PIP 2 by upregulating the expression of *P15K* gene. Increase in PIPK isoforms expression contribute to increased conversion of PIP 2 to two important molecules, of diacylglycerol and inositol 1,4,5-trisphosphate (IP3). Diacylglycerol and IP3 are important secondary messengers that are able to stimulate protein kinase C and finally release trigger Ca^{2+} release.

Abiotic Stress Responses: Genome Wide Expression

Abiotic stresses causes increase of many intracellular substances, also affects nucleic acids, proteins, carbohydrates and amino acids. Molecular biology techniques introduction in plant biology enables an immense effort towards the identification of stress-inducible genes. Molecular studies thrive in isolating genes that were known to function in stress responses and tolerance. It is now known that transcriptional activation happens at different time points in response to stress stimuli. This suggests that abiotic stress responses are very complicated is controlled by a various signalling means and different transcription factors. Identification of many significant factors in the stress pathway had been able to use responsive genes as markers. For example, dehydration responsive element (CRE)/C-repeat (CRT) (A/GCCGAC) an abiotic stress-responsive cis-element, and its post-translational modifications were recognized, which in turn has increases the scope of research that play central role in identifying the transcriptional regulating factors (Shinozaki and Yamaguchi-Shinozaki 2007). Also the genetic screening for mutations affects the expression of stress inducible genes thus enabled the identification of novel components in the abiotic regulatory system (Chinnusamy et al. 2002).

Completions of the genomes of *Arabidopsis* and *Oryza sativa* have also added to the information available on stress physiology. The absolute genome sequence is now-a-days accessible and also has enabled genome-wide gene expression profiling to a variety of abiotic stresses (Kilian et al. 2007). Microarray technology has also enabled the knowledge of genes responding to abiotic stresses that have been identified more in detail than before. Complete transcriptome analysis have facilitated the relationships between stress-regulated transcripts, and their regulatory elements (Weston et al. 2008). The function of stress-inducible genes can also be determined by the reverse genetic approach, assisted by insertion mutation lines.

Vast microarray experiments have lead to the identification of the regulators for stress-inducible intracellular signalling and gene expression of various types of transcription factors (e.g. MAP kinases, phosphatises and metabolic phospholipid enzymes). This classification of inducible stress signal transducers augmented an thought that plants have developed transformable cellular response means to resourcefully react to various abiotic stresses.

Metabolic Profile Under Abiotic Stress

Metabolism reveals biological activities dependent on the environmental conditions. Study of metabolic profile under abiotic stress conditions has made possible the detection and recognition of metabolites. Under stress conditions, plants reorganize their metabolic pathways in order to adapt to changing conditions (Kaplan et al. 2004). Using these metabolic profile changes as a marker, metabolic movements and factors that regulate them were analysed in combination with other 'omic' analyses, such as transcriptome particularly through mass spectrometry-based analytical methods (Saito et al. 2008; Sawada et al. 2009). The metabolic pathways often employed from vital primary metabolism pathways, upon initial gene duplication, play main part in the plant and environment communication (Nascimento and Fett 2010). Accordingly, the diverse growth surroundings have a major impact on the synthesis and accrual of secondary plant products. Therefore, this production of secondary plant products acts as a surviving response for plants to manage the increasing stress. There are varieties of secondary products synthesized during these processes and are listed below.

Phenolic Compounds

A large variety of secondary products produced by plants contain a phenol group, a hydroxyl functional group on an aromatic ring called Phenol, a chemically heterogenous group. This group forms an important part of the plants defence system against biotic and abiotic stress condition. Increase in salt concentration increases the total phenolic content of leaves (Savirnata et al. 2010). Flavinoids form one of the largest classes of plant phenolics that carry out extremely dissimilar functions in plant coordination also including defence and pigmentation (Kondo et al. 1992). Like flavonoids, anthocyanins also have multiple biological activities as antioxidant component.

Isoflavonoids are derivatives of flavonone intermediate, naringenin that occurs universally in plants. They are known to be released by the legumes playing an important part in encouraging the creation of nitrogen-fixing nodules by symbiotic rhizobia (Sreevidya et al. 2006). Besides this they also participated in plant growth and defence responses. Studies done by Posmyk et al. (2009) observed that the production of these flavonoids is an efficient approach against ROS.

Alkaloids

About 20% of the species of vascular plants has substantial members of N-containing secondary metabolites. Most of alkaloids include pyrrolizidine alkaloids (PAs). They are considered to be toxic and primarily serve as defence against herbivoral attack (Schafer and Wink 2009). But under highly suppressive conditions these alkaloids play role as ROS scavengers. Studies have also shown that ROS production also regulates the alkaloid pathway occurring in undifferentiated cells. It seems they also have mechanisms for directing the alkaloid pathway in other parts of the plants (Sachan et al. 2010).

Influence of Salt Stress on the Synthesis of Secondary Plant Products

Salt stress is one of the serious factor that limits the efficiency of crops and especially quantity and quality of their metabolic (secondary plant products) products. Against the attack of pathogens, plants manufacture secondary plant products as a part of defence mechanism. Therefore, the concentrations of large amount of secondary products are totally dependent on the surrounding environmental circumstances. High salt concentrations in the soil are accountable for the production of the secondary plant products by making a major change in the metabolic enzymes/pathways. Volatile sulphur compounds, vitamins, carbonyl compounds, ascorbic acid and flavonoids are some of the active secondary metabolities that are stimulated under environmental stresses (Krasensky and Jonak 2012). Enzymes like Phenylalanine ammonium lyase (PAL) and Glutathione-S-transferase (GSTs) also get induced from unfavourable effects of stresses (Marrs 1996). PAL, in action with cinamates 4-hydroxylase forms essential group of enzymes that helps in biosynthesis of several important secondary metabolites from phenyl alanine (Singh et al. 2009). In a series of experimental observations, it could be shown that plants which are exposed to salt stress produce a greater amount of secondary plant products such as phenols, terpenes as well as N and S containing substances such as alkaloids, cyanogenic glucosides or gluco-sinolates (Singh et al. 2009).

Metabolomics: Recent Technology Developments and Applications

Plants are known to be nature's excellent chemists, as they have a huge variety of chemical substances that fit according to the needs of a highly variable and generally hostile environment conditions (Baxter and Borevitz 2006). Natural metabolic range and a lack of combination of principles require identification of compounds, forming major analytical challenge (Breitling et al. 2006). As, metabolomic applications in

crop/plant analysis are constantly growing, therefore the use of liquid chromatography mass spectrometry (LC-MS), GCMS and NMR are greatly explored to get more full insight into the variation of compositions in the metabolites. Research in potato using flow injection mass spectrometry analysis (FIMS) of a varied range of genotypes, showed the correlation between genotypes with different traits in free amino acid content (Beckman et al. 2007). Metabolomic technologies facilitate the multivariant metabolic data using varied, chromatographic detection systems, such as GC-MS, Fourier-transformed infrared spectroscopy/NMR-based methods.

Techniques like Matrix-assisted laser desorption/ionization (MALDI-TOF) and GC-MS profiling revealed dissimilarity in metabolic composition like amino acids and organic acids in tomato cultivars even though these cultivars were closely related (Fraser et al. 2007). Thus, the excellence of crop/plants nutritional value is the expression of metabolite content (Memelink 2004). There is therefore great importance of using a metabolomics approach to know better what in particular has happened during stress encroachment and provide help to plan new ideas for crop improvement.

Metabolomics is entirely positioned to perceive the pathway that drive the expression of a trait and potentially enable breeders, to select the desired trait of superiority for high-yielding varieties also with tolerance to abiotic stress. Plant's response to salinity involves changes in the functionality of genes and proteins that consistently lead to changes in plant metabolism. Gas chromatography time-of-flight mass spectrometry outlines the novel details from the plant models, Rice, *Arabidopsis thaliana and Lotus japonicus* that demonstrated the power of metabolite profiling providing insight to disturbed cellular balance between amino acids and organic acids in response to salt stress.

Because of the highly assorted nature of metabolites, metabolome analyses are subjected to combination of technological and analytics. The most noteworthy advantage of metabolome analyses is the static chemical uniqueness of metabolite entities. In comparison to genomics, transcriptomics and proteomics analyses that enables the identity of genes and proteins, metabolomics provide highly appropriate investigations of metabolic, like the physiological responses caused by environmental perturbations (Desbrosses et al. 2005).

This data-rich analytical advancement have ignited the development of bioinformatic tools to sort through the complex fingerprints and profiles of data sets for relevant descriptive information. More specifically, bioinformatics with metabolite fingerprinting and profiling approaches grant access to the eventual biological information flow between gene expression and metabolic phenotype.

Some studies on higher plants upon exposure to salt stress utilize profiles of metabolic fingerprinting to explore changes in them. The metabolic impact of salt stress have been studied in crops like *Lycopersicom esculantum*, *Solanum lycopersicon*, *Oryza sativa*, *Vitis vinifera* and the model plant *Arabidopsis thaliana* (Cramer et al. 2007; Kim et al. 2007; Zuther et al. 2007). Comparisons of metabolite profiles have also been carried out in halophytic species, such as the *Populus euphratica* tree or the shrubs *Limonium latifolium* and *Thellungiella halophila* (Gong et al. 2005; Gagneul et al. 2007).

Analysis of the FT-IR spectra, provided information on compound classes specific that revealed signals from nitriles and amino radicals and some nitrogen containing compounds allowing the comparison between control samples and salt-treated fruits,

leading to a clear classification of the investigated cultivars of *S. lycopersicon*. Another study on the salt-tolerant tree *P. euphratica* in combination with transcriptomics and GC-MS based metabolomic analyses revealed that within the natural habitat of plants, they are acclimated to the environment. It was observed that there was an increase in amino acid levels, specifically proline, valine and b-alanine, changes in sugar and polyol metabolism this may be due to high sodium concentration in the field. Increase in the levels of myo-inositol, glyceric acid and glycerol were reported while a decrease was observed in levels of fructose and mannitol (Brosché et al. 2005).

Study by Gong et al. (2005) where the transcriptional and metabolic profiles were investigated in the glycophyte *A. thaliana* to short term salt stress in comparison to halophyte *T. halophila*. An interspecies difference was demonstrated by GC-MS-based metabolite profiling that moderately amplified during response to 150 mM NaCl salt shock. Surprisingly, constant group of numerous metabolites and transcripts that are stress-responsive were found to be already changed in *T. halophila* even before exposure to salinity, signifying a continuous adjustment mechanism in halophytic species. Also, research have shown that sugars along with proline, citric acid, malic acid and succinic acids were reportedly higher in halophyte *T. halophila* than in *A. thaliana*.

Cramer et al. (2007) explored and compared the transcriptome and GC-MS-based metabolomic profile of drought and salt stress shoot tips from *V. vinifera* cv. Cabernet. It was revealed from metabolomics, sucrose, aspartic, succinic and fumaric acids levels reduced. The profile of proline, asparagine, malic acid and fructose showed increase in their levels under salt stress. Further, under water-limited conditions most metabolites exhibited similar trends, in contrast to glucose, malic acid and proline which increased noticeably. Recently, the role of the compatible solutes was also studied in the halophytic species *L. latifolium*, by means of untargeted and targeted metabolic profiles (Gagneul et al. 2007). It was noticed that sugars, inositols and proline acted as osmolytes balancing the cell environment, while organic acids decreased upon salt stress.

Investigations by Sanchez et al. (2008) during salt stress in legume plant *Lotus japonicus* used an combination of transcriptomics, ionomics and metabolomics technique, thereby found a vast enlargement in the constant levels of many amino acids, sugars and polyols, with a simultaneous reduction in accumulation of most of the organic acids. It was thus suggested that, metabolic responses during increased salinity showing changes in organic solute composition are there by guarded by adaptive developmental programs, that be inferred to metabolic anticipation of stress.

Conclusion and Future Perspective

It can be concluded from past and present metabolomic studies of plant response towards salinity is that; the changes occurring in metabolism are complex and therefore involve multiple pathways. Particularly during acclimation of salt stress the response is coupled with changes in metabolism of organic acid, amino acid and sugar. The changes

that appear are in the form of primary metabolism that overlaps with the reaction of other interacting/regulatory stress factors. These traits are accompanied with a broad array of response at the whole-plant level (molecular and cellular). Metabolomics is coming up as one of the key tools in studying plant stress responses in the direction of gene expression individually/in group. Metabolic networks are highly dynamic particles and they keep on moving from one cellular compartment to another. Given that the metabolic profiling enables the better understanding of the unchanged level of metabolites, kinetics and flux analyses. It also adds to the knowledge of the unpredictable metabolic changes occurring towards stress. Metabolic examination at the plants-subcellular level in specific tissues plays a part for future challenge. Significant new discoveries in metablomics have enhanced the field. Combination of metabolomics, proteomics, transcriptomics and mathematical modeling in future will provide us an insight on how plants respond to salt stress and thus will enable us to develop strategies for enhancement towards the stress tolerance in plants.

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