Chapter 9
Cross-talk of Compatible Solutes with Other Signalling Pathways in Plants

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Abstract Plants when exposed to varying level of abiotic stress conditions undergo a large number of changes at the physiological and molecular level that considerably affects their growth and development. Abiotic stresses affect cellular homeostasis and enhance generation of reactive oxygen species which ultimately leads to earlier senescence in plants. In response to stress conditions, plants accumulate enhanced level of osmolytes in coordination with different stress signalling pathways. This chapter discusses interaction of osmolytes and different signalling molecules and their role for survival of plants under stress conditions. Studies related to biosynthesis pathways of osmolytes have helped to identify novel candidate genes that regulate the stress response in plants.

Keywords Stress · Osmolytes · Signalling · Accumulation · Pathways

9.1 Introduction

Plants are exposed to tough environmental stress of temperature, drought, salinity and heavy metals that generates reactive oxygen species which hampers cellular and developmental processes. To save plants from damage caused due to oxidative stress, accumulation of compatible solutes occurs to maintain normal structure and functions of cellular machinery (Fig. 9.1). Most common osmolytes are proline, glycine betaine, polyamines and sugars, which protect plant cells by interfering with the generation of ROS like hydroxyl and superoxide ions, free radicals and peroxides. Initially, stress signals are sensed by definite receptors proteins present

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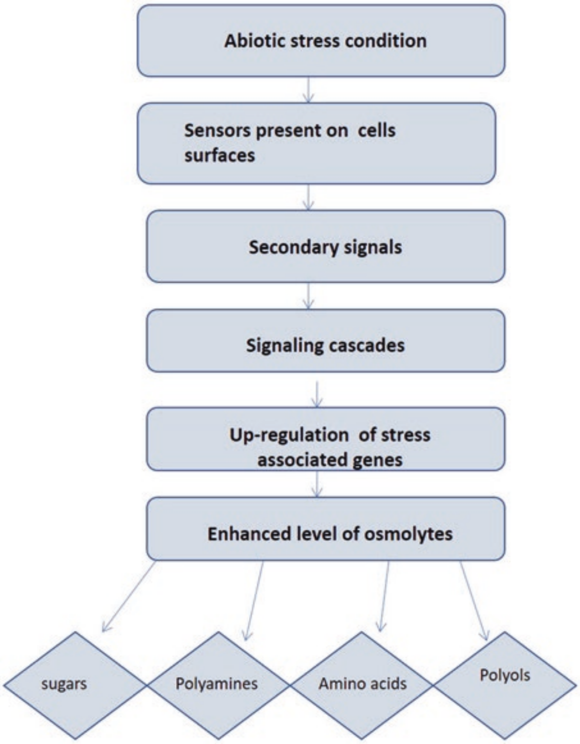

Fig. 9.1 Schematic mechanism of abiotic stress response on plants leads to enhanced accumulation of osmolytes. Stress signal activates signalling cascade, which up-regulates stress-responsive genes related to accumulation of osmolytes to make stress-tolerant plants

on the plant cell surfaces. These receptors further transmit received signals to nucleus where transcription factors up- or down-regulate the level of expression of genes associated with stress tolerance, which codes for various defensive and adaptive proteins. Common signalling agents in plants are Ca^{2+}, inositol phospholipids-proteins, cyclic nucleotides, kinases and protein phosphatases. The signalling pathway in plants involves the organization and harmonization of more than one signalling molecule in diverse cellular compartments and regulates different biochemical and physiological responses. There exist highly efficient cross-talk between various signalling pathways to connect different network cascades for signal transduction. Each pathway in these cascades involves multiple proteins: numbers may vary between few hundred to thousands. Earlier, signal transduction pathways were thought to be linear cascades, but with recent advances in database accessibility based on genomics and bioinformatics information gathered from transcriptome profiling, mutagenesis data, and plant 'omics,' it is now possible to understand interactomics between these molecules. This mechanism of coordination can be described as "cross-talk" and "network." Signalling molecules or intermediates when shared between two or more signalling pathway are said to be a case of direct cross-talk. Indirect cross-talk is a case of chronological reactions, where the function of first pathway is used for the activity of second pathway. During signalling cascades, critical components which make this machinery are ion channels, signalling proteins and second messengers that regulate early events in this pathway.

9.2 Signalling Cascades for Osmolytes Production

Drought, salinity and low temperature stress are complex phenomena; their individual effects on plants had many different attributes, but these stresses still have few related properties and cause similar kind of disturbances inside the cells. For example low temperature changes activities of some macromolecules and also reduces osmotic potential inside the cells. Similarly salinity stress also disturbs ionic and osmotic factors inside the plant cells. Under normal conditions, sensor present on plant cell surfaces detects stress-related change and initiates a cascade or stepwise reactions inside the cells. There may be a single and sometimes multiple primary sensors which sense initial signals induced under different stress conditions. Stress signal was initially received by primary sensors like histidine kinases and later transferred to transcriptional factors like MYC/MYB, AREB/ABF, DREB, etc. which regulate expression of genes involved for osmolyte biosynthesis. Secondary signals include hormones and messengers that trigger or activate the next series of events during this signalling cascade. Their receptors may be embedded at some locations within the cells which were different from that of primary sensors. Secondary signals involve interaction or cross-talk among different signalling pathways in response to different stresses. In plants, molecules which act as secondary messenger include mainly Ca^{2+}, IP_3 and cyclic GMP (cGMP). Ca^{2+} ion is a crucial molecule during signalling process and a common point for different signalling pathways (Tuteja and Mahajan 2007). In all eukaryotic cells, Mitogen-activated protein kinase (MAPK) works during transduction of stress signals by phosphorylation of other targets molecules like kinases, enzymes and transcription factors on serine or threonine amino acid. Plant hormones like auxins, abscisic acid, jasmonic acid, salicylic acid, ethylene and brassinosteroids influence signalling process by MAPK cascades (Hettenhausen et al. 2014; Lu et al. 2015).

MAPK cascade consists of three stepwise protein phosphorylation working on component serine/threonine kinases, a MAP kinase kinase kinase (MAPKKK), a MAP kinase kinase (MAPKK) and finally, the MAP kinase (MAPK), by inducing activation and phosphorylation of subsequent kinases in a cascade. The MAPK pathways get triggered by various receptors like tyrosine kinases, G-protein–coupled and two-component histidine kinases kind of receptors. Several putative sensory kinases will helps us to identify intermediates involved which will determine if the kinase signalling involved is specific or there are cross-talks between these pathways. Some members of MAPK cascades are activated by multiple stresses which suggests working of MAPK cascades as points of common junction during stress signalling.

The hormones or growth regulators in plants affect numerous physiological and developmental processes, beside this hormone affects plants nutritional status and response of the target cell to different environmental changes. Enhanced levels of osmolytes protect plants by minimizing damages and rescue them from oxidative damage caused by stress conditions.

9.3 Compatible Solutes

During stress, plants accumulate osmolytes like L-proline, glycine betaine (GB), glycerol, mannitol, sorbitol, etc. (Sharma et al. 2019, Rasool et al. 2013; Gupta and Huang 2014).Compatible solutes are soluble organic compounds with low molecular weight, which accumulate in plants cells cytosols. During stress conditions, these osmolytes change interaction chemistry of proteins with DNA by linking themselves with the nucleic acid (Kurz 2008). Most common classes of compatible solutes are betaines, sugars (glucose, fructose, fructan, etc.), sulfonium compounds, polyols (mannitol, glycerol, sorbitol), polyamines (spermine, spermidine and putrescine) and amino acids like proline and glutamine (Slama et al. 2015; Pathak and Wani 2015; Sah et al. 2016).

Plants accumulate compatible solute to stabilize proteins and cellular organelles by making osmotic adjustment and regulating redox metabolism for removal of excess ROS level and maintain redox balance in plant cells (Chinnusamy and Zhu 2009; Krasensky and Jonak 2012).The osmolytes accumulation is regulated by various hormones like abscisic acid, brassinosteroids, cytokinins, ethylene, jasmonates and salicylic acid. In this chapter, we will try to discuss mechanisms and understand the role of phytohormones for the osmolytes accumulation in response to abiotic stresses in plants.

9.4 Molecular Mechanism to Understand Cross-Talk

9.4.1 Glycine Betaine Biosynthesis

GB accumulates in response to abiotic stresses in plants. Glycine betaine is soluble quaternary ammonium component that does not cause toxicity inside cells (Cleland et al. 2004). Glycine betaine had ability for membrane stabilization, protects photosystem II and alleviates oxidative damage caused due to stress conditions (Chen and Murata, 2011). Glycine betaine bio-synthesis can be divided into two types on the basis of initial precursor used and enzymes involved during the reactions (Sakamoto and Murata 2000). GB synthesis takes place by using two different substrates: choline and glycine. Glycine betaine is synthesized by the oxidation of choline in two-step process catalyzed by separate enzymes. The enzyme responsible for catalysis of first step is choline monooxygenase (CMO) (Rathinasabapathi et al. 1997). Catalysis of other step is controlled by betaine aldehyde dehydrogenase (BADH) (Wood et al. 1996; Fitzgerald et al. 2009). The CMO and BADH expression was triggered by various stress conditions like salt (McCue and Hanson, 1992), drought (Li et al. 2016), cold (Xing and Rajashekar 2001) and heat (Mitsuya et al. 2011). ClCMO and ClBADH genes have a CGTCA-motif in their promoters which is responsible for response to hormonal signals like methyl jasmonate, ethephon, Abscisic acid and Salicylic acid which is further effective in inducing the expression of ClCMO and ClBADH genes, and glycine betaine accumulation in plants.

9.5 Glycine Betaine and Hormone Response

Enhanced level of ethylene synthesis is associated with abiotic stress responses in plants (Morgan and Drew 1997). First important step during ethylene synthesis is synthesis of S-adenosylmethionine from methionine. The SAM created during this reaction also works as precursor during biosynthesis of glycine betaine. Cross-talk between two pathways was experimentally proved by Khan et al. in 2014. They described that when salicylic acid is applied exogenously in *Vigna radiata* plants exposed to salt stress, it showed increased methionine concentration and accumulated GB. Enhanced concentration of glycine betaine and lower ethylene level during salt stress increased the glutathione (GSH) levels which resulted in lower oxidative stress damage. In tobacco and tomato, ethylene level was enhanced in response to cold stress, without any accumulation of GB (Park et al. 2004). Whereas in bean and wheat, Glycine betaine accumulates, while ethylene production decreased during cold stress (Wang et al. 2010). This type of reverse behaviour between ethylene and glycine betaine accumulation can be explained by the mechanism of donation of methyl group from SAM to choline, common link between the two biosynthesis pathways (Kurepin et al. 2015). Direct involvement of ethylene in mitigating light stress is less, however endogenous ethylene controls the synthesis of GB, which alleviates light stress-induced responses in plants. Brassinosteroids, when provided exogenously, show increased accumulation of glycine betaine and help in tolerance to stress as shown in Table 9.1 for some important crop plants. Studies using seven-day-old plants of *Raphanus sativus,* when exposed to Cr stress and treated with 24-epibrassinolide, exhibit enhanced glycine betaine level and expressed increased tolerance for Cr stress (Choudhary et al. 2011). BR-stimulated glycine betaine accumulation might be attributed to increased catalytic activity of betaine aldehyde dehydrogenase (BADH) (Rattan et al. 2014).

9.6 Proline Biosynthesis

Proline is an amino acid and a molecular chaperone that scavenges free radicals generated during abiotic stress in plants. In control conditions, proline plays important role in developmental process of seeds and embryo (Mattioli et al. 2009). Proline stabilizes secondary structures of proteins (Funck et al. 2012) and also serves as a reservoir for storing cellular carbon and nitrogen during the plant recovery phase (Kavi Kishor et al. 2005).

Table 9.1 Showing effect of different signalling molecules on osmolytes accumulation

Plant species	Stress	Signalling hormone	Response	References
Prunus persica fruits	Chilling injury(cold storage)	24-epibrassinolide	Increased proline level and also of Δ1-pyrroline-5-carboxylate synthetase (P5CS)activity	Delauney et al. (1993)
Raphanus sativus	Cu and Cr stress	24-epibrassinolide	Significant increase in proline content	Sharma et al. (2011) and Choudhary et al. (2010)
Salvia miltiorrhiza	Drought stress	Foliar spray of BR	Enhanced proline content	Zhu et al. (2014)
Cucumis sativus	Cu stress	24-epibrassinolide	Enhanced proline content	Fariduddin et al. (2013)
Capsicum annuum var. *frutescens*	Water stress	Foliar spray of BR	Significant increase in proline content	Khamsuk et al. (2018)
Brassica juncea	Copper stress	Synthetic BR	Enhanced proline level	Fariduddin et al. (2009)
Raphanus sativus	Cr stress	24-epibrassinolide	Enhanced level of glycine betaine	Choudhary et al. (2011)
Pisum sativum	Salt stress	24-epibrassinolide	Enhanced glycine betaine content	Shahid et al. (2014)
Tomato plants	Salt stress	24-epibrassinolide	Increased level of glycine betaine	Ahmad et al. (2018)
Pisum sativum	Cd stress	24-epibrassinolide	Enhanced glycine betaine content	Jan et al. (2018)
Triticum aestivum	Heat stress	SA (0.5 mM)	Increasing the content of proline	Khan et al. (2013)
Rauvolfia serpentina	Salt stress	Salicyclic acid	Increasing the content of proline	Misra and Misra(2012)
Torreya grandis	Salt stress	Salicyclic acid	Enhanced proline level	Li et al. (2014)
Brassica juncea	Heat stress	SA treatment	Enhanced proline level	Hayat et al. (2009)
Dianthus superbus	Salinity stress	SA treatment	Elevation in proline content	La et al. (2019)
Vigna radiata	Salt stress	SA	Glycine betaine accumulation	Misra and Misra (2012)
Triticum aestivum	Water deficit	GB and SA	Glycine betaine accumulation	Aldesuquy et al. (2012)
Helianthus annuus	Drought stress	GB and SA	Glycine betaine accumulation	Hussain et al. (2009)
Glycine max	Salinity stress	Salicyclic acid	Elevation in level of methionine, tyrosine and phenylalanine	Farhangi-Abriz and Ghassemi-Golezani (2016)

(continued)

Table 9.1 (continued)

Plant species	Stress	Signalling hormone	Response	References
Abelmoschus esculentus	Water deficit	Salicyclic acid	Elevation in amino acid	Sankar et al. (2007)
Sorghum bicolor	Water deficit,	Salicyclic acid	Elevation in amino acid	Yadav et al. (2005)
Helianthus annuus	Cu metal stress	Salicyclic acid	Elevation in amino acid	El-Tayeb et al. (2006)
Zea mays	Salinity	Salicycic acid	Proline and GB content	Hussein et al. (2007)
Quinoa	Drought	Salicycic acid	Enhancement in amino acid content	Abd Allah et al. (2015)
Brassica napus	Cold stress	Abscisic acid	Enhancement in the level of proline	Burbulis et al. (2010)
Cicer arietinum	Cold stress	Abscisic acid	Increased level of proline	Kumar et al. (2008)
Cynodon dactylon	Cold	Abscisic acid	Increased proline content	Cheng et al. (2016)
Medicago sativa	Drought	Abscisic acid	Enhancement in the level of proline	An et al. (2014)

Synthesis of proline occurs from either glutamate or ornithine (Fichman et al. 2014) in higher plants. Proline during synthesis from glutamate needs bifunctional enzyme $^{1}\Delta$-pyrroline-5-carboxylate (P5C) and synthetase (P5CS) for reactions that uses ATP and NADPH for generation of glutamate-γ-semialdehyde. Increased proline levels is a strong indication of stress tolerance because of their dynamic role for chlorophylls reconstruction and participation for establishment of Kreb's cycles intermediates (Ashraf and Foolad 2007; Ahmad et al. 2015).

9.7 Proline and Hormone Response

During drought conditions, *P5CS1* (pyrroline-5-carboxylate synthetase 1) expression level was increased, when exposed to drought stress the level of *P5CS1* was enhanced in control plants but it remains unaffected in case of *ein* mutants (Cui et al. 2015). Recently, Iqbal et al. (2015) explained interrelationship between proline and ethylene to provide salinity tolerance in *Brassica juncea*. Iqbal et al. (2015) reported that N regulates proline production and ethylene formation to alleviate salinity stress. Chrominski et al. in 1989 described increased change of ACC into ethylene on exposure to salt and water stress in *Allenrolfea occidentalis* and explained that under such conditions, exogenously applied proline balances level of ethylene in these plants.

Salicycic acid is reported to be engaged for enhancing proline content under abiotic stress in plants (Khan et al. 2013). *Lens esculenta* plants when treated with

0.5 mM of Salicyclic acid under salt stress showed improved activity of proline synthesis enzymes. Exogenously applied proline causes enhanced accumulation of salicyclic acid endogenously (induced by NDR1-dependent pathways) and regulates Ca-mediated oxidative stress for plant defence (Chen and Murata 2011).

Jasmonic acid (JA) regulates water potential in plant cells under various abiotic stress conditions. Shan et al. (2015) described that JA alleviates drought stress by the proline biosynthesis. JA is responsible for up-regulation of key genes involved during adaptation response by increasing synthesis of secondary metabolites and stress-responsive proteins along with enahnced proline level (Abdelgawad et al. 2014). Jasmonic acid–induced changes in the proline level had been explained in several stress-based studies like heavy metal (Farooq et al. 2016; Poonam et al. 2013) and salt stress (Yoon et al. 2009). Jasmonic acid when applied exogenously increases level of organic intermediates formed during kreb cycle which include citrate, succinate, fumarate and malate which are responsible for providing abiotic stress tolerance in plants (Sharma et al. 2018).

Abscisic acid contributes significantly to control proline metabolism in plants during abiotic stress (Kumar et al. 2012). ABA enhances proline content in plants to protect from stress conditions (Sarafraz et al. 2014; Karimi and Ershadi 2015; Sarafraz-Ardakani et al. 2014). ABA increases the genes transcript levels which code for enzymes of proline biosynthetic pathways (Sripinyowanich et al. 2013).In *Medicago truncatula*, proline synthesis during drought stress was regulated by ABA signals (Planchet et al. 2014). ABA signalling controls proline biosynthesis in abiotic stress in plants (Pal et al. 2018; Verslues and Bray 2006).

9.8 Ethylene Role in Stress Signalling

Ethylene, a gaseous phytohormone, affects germination of seeds, developmental process in plants, senescence in case of leaf and flower, ripening of fruits and impacts abiotic stress tolerance (Osborne 1993). Iqbal et al. (2015) reported role of ethylene to regulate abiotic stress response by showing its effect on accumulation of osmolytes. Studies involving mutant of *ein2–5* and *ein3–1* (ethylene insensitive) confirmed role of ethylene during biosynthesis of osmolytes (Cui et al. 2015). Expression of pyrroline-5-carboxylate synthetase, during proline biosynthesis, was enhanced in the plants which were exposed to drought stress in comparison to control plants, but remained unaffected in *ein* mutants.

9.9 Carbohydrates

In plants, sugars work as chief energy source, but also perform other regulatory functions like signalling for regulating development and metabolic activity in plants. There is a tight link between sugar signalling and hormone signalling, which controls growth, development and stress reaction in plants. Sugars play important role during stress tolerance as powerful compatible solutes that help plants for conservation of water inside the cells, thus decreasing water access for nucleation in the apoplast (Ruelland et al. 2009). Disaccharides like sucrose, trehalose, raffinose family oligosaccharides and fructans actively participate in stress tolerance in plants (Keunen et al. 2013). Miranda et al. in 2007 studied how during cold acclimation in *Arabidopsis*, level of soluble sugars (trehalose) enhanced noticeably. Initial reaction in response to drought stress is observed with enhanced levels of monosaccharides, while delayed response is connected with increase in the fructans level (Kerepesi and Galiba 2000). Trehalose accumulation was reported in some desiccation-tolerant plants, since it has unique tendency to acts as substitute of water on the surface of macromolecules. Flowers (2004) detailed its role in ROS scavenging and signal cascades. Fructans have high water solubility and resistance to crystallization at subzero temperatures and the ability of the synthesis pathway of fructan to work normally even at low temperature conditions (Livingston et al. 2009). During drought stress, glucose provides desiccation stress tolerance by inducing closure of stomata (Osakabe et al. 2014). During water deficiency, sugar accumulation protects oxidation of cell membranes (Arabzadeh 2012).

Sugars function as osmoprotectant to reduce the harmful effects of salt stress on plants (Almodares et al. 2008). Rosa et al. in 2009 proved that noticeable augmentation in the level of glucose, sucrose and fructose occurs during salinity which is responsible in maintaining osmotic balance inside the cells. In case of wheat studies have shown that application of even low glucode level during seedling stage resulted in considerable enhanced germination even when the plants are exposed to high level of salinity.

Glucose when applied exogenously during salt stress results in increased dry weight, helps to maintain ionic balance, helps in accumulation of proline and prevents water loss (Hu et al. 2012). In higher plants, different soluble sugars, like glucose, sucrose, raffinose and stachyose, provide tolerance to freezing temperature (Yuanyuan et al. 2009). Fructans because of higher water solubility prevent crystallization of water during chilling stress (Livingston et al. 2009). In rice, trehalose content is enhanced during cold stress (Garg et al. 2002). Soluble sugars are connected with anabolism and catabolism of ROS; pentose phosphate pathway that is involved in NADPH production is involved in ROS scavenging (Hu et al. 2012). Exogenous application of glucose at lower level prevents peroxidation of lipids during NaCl treatment (Hu et al. 2012). Lower level of sugars like glucose and sucrose activates antioxidant enzymes during salt stress (Boriboonkaset et al. 2012). When applied exogenously, low nitrogen along with glucose up-regulates senescence-related gene expression level to about hundred-folds. Accelerated leaf senescence occurs due to hexokinase-based signalling mechanism (Wingler et al. 2006). In *Arabidopsis*, trehalose-6-phosphate synthase activity results in enhanced flowering (Gibson 2005).

9.10 Sugar as a Signalling Molecule

Plant growth regulators like ABA, gibberellins and kinins regulate sugar metabolism and its translocation to different locations during stress conditions (Gibson 2004). During germination, glucose works as powerful modulator for regulating expression of genes related with ABA synthesis (Price et al. 2003; Xu et al. 2010) and also suppresses ABA catabolism genes (Zhu et al. 2009). Application of glucose in *Arabidopsis* induced increased expression of ABA, like ABA2, ABI1 and ABI4 genes (Price et al. 2003). Cheng et al. in 2002 examined that higher glucose concentration up-regulates level of ABA biosynthesis genes like ABA2 and NCED3 (Cheng et al. 2002). In rice, OsNCED genes which are five in number and three ABA8'-hydroxylase (OsABA8ox) genes are involved in both synthesis and catabolism of ABA (Zhu et al. 2009). In higher plants, higher glucose level and ABA are known to arrest development of seedlings (Dekkers et al. 2008). A complex relationship exists between glucose and different hormones, like abscisic acid and ethylene (Cheng et al. 2002; León and Sheen 2003). During germination of seeds, ethylene antagonizes the negative effect of higher level of glucose. Ethylene shows opposite role in comparison with ABA during germination (Beaudoin et al. 2000). Negative type of correlation was observed with the exogenous application of sucrose (Xu et al. 1998). In barley and rice, exogenously applied glucose decreased gibberellins level (Gibson 2005). Cytokinins are responsible for causing decrease in glucose concentration by activating invertase enzyme that helps in utilization of sugars and is responsible for causing delay in senescence.

9.11 Amino Acids

In plants, amino acid concentration increased during abiotic stress (Lugan et al. 2010). Amino acids involved in stress tolerance include proline, alanine, glycine, glutamate, aspargine, γ-aminobutyric acid (GABA), citrulline, ornithine, etc. Three major types of polyamines are putrescine (Put), spermidine (Spd) and spermine (Spm), but some other forms of PAs, like cadaverine, may also be there in some cases. Polyamines have strong affinity to bind with nucleic acid and proteins via electrostatic linkages. These amino acids function as osmolytes and sometimes act as precursors also. In plants, PAs regulate very important physiological processes like senescence, developmental process, cellular proliferation, signal transduction and control gene expression for traits which cause different types of responses under stress conditions (Alcázar et al. 2006).

In some cases, three most common polyamines, Put, Spd and Spm, show considerable increase after exposure to abiotic stress (Yang et al. 2007). In majority of cases during abiotic stress only single type of polyamines showed considerable increase in the level of expression. Callus formed during Apple tissue culture on treatment with salt stress exhibited enhanced Put levels, while very minor changes were observed in the level of Spd and Spm (Liu et al. 2006). Sweet orange callus shows enhanced level of Spd after exposure to salt and cold stress for a brief duration (Wang and Liu 2009). In *Vitis vinifera* also sharp enhancement of Spd and Spm occurred during salt stress (Ikbal et al. 2014). Increased heat stress tolerance in alfalafa was attributed to enhanced level of spd and decreased level of put and spm amino acids (Shao et al. 2015). Biosyntheses of polyamines and ethylene are interconnected by SAM, which is a common precursor for both the reactions. Metabolism of polyamines affects nitric oxide generation also (Yamasaki and Cohen 2006). Polyamines induce formation of NO which works as common linking point for polyamine-mediated stress response and intermediaries involved during different stress mechanisms (Tun et al. 2006).

9.12 Gamma-Aminobutyric Acid (GABA)

GABA is a non-protein type of amino acid; it is produced during different abiotic stress conditions. The α-ketoglutarate is the precursor for GABA biosynthesis, which gets converted with the help of glutamate dehydrogenase to glutamate; another enzyme, glutamate decarboxylase, converts glutamate to GABA. During unfavourable conditions, GABA helps to maintain osmotic balance and regulates pH, nitrogen metabolism and prevents ROS build-up in plant cells (Barbosa et al. 2010; Renault et al. 2010).

GABA accumulates during high salinity level (Zhang et al. 2011; Renault et al. 2010) in plants. Flood stress causes reduction of cytosolic pH and oxygen deficiency, which causes increased GABA accumulation (Kinnersley and Turano 2000). Stress conditions like cold, heat, salt and other environmental stresses increase Ca^{2+} levels inside the cells, which can activate calmodulin-dependent GABA synthesis (Kinnersley and Turano 2000). Exogenous application of GABA in case of *Caragana intermedia* changes gene expression in roots which are exposed to NaCl stress and activates different pathways which have a role to play during signalling cascades.

9.13 Conclusions

Abiotic stress is one of the main restrictive factors responsible for decline in crop production. Plants have devised new strategies to overcome these environmental stresses. Technological advancement during the last three decades by use of molecular and genomic approaches provides stronger means to study molecular, and physiological, aspects regarding stress signalling in depth. This chapter briefly covers the knowledge of different intermediates involved during signalling metabolism, the signals which activate osmolyte accumulation and maintain their distribution during stress and also discusses the role of enzymes responsible for osmolytes synthesis and degradation. a Comprehensive scenario of functions of different osmolytes and their interaction networks in different environmental conditions was also discussed. Future focus of researchers will now be to explore and establish benefits of osmolytes to regulate crop improvement. To achieve this goal, recent developments in plant genetic engineering using genome editing will prove useful for generating genetically superior crops, with improved ability to accumulate osmolytes during stress conditions.

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