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REVIEW

Nitrogen containing compounds and adaptation of plants to salinity stress

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Abstract

A number of nitrogen containing compounds (NCC) accumulate in plants exposed to salinity stress. The most frequently accumulating NCC include amino acids, amids, imino acids, proteins, quarternary ammonium compounds (QAC) and polyamines. The specific NCC that accumulate in saline environment vary with the plant species. Osmotic adjustment, protection of cellular macromolecules, storage form of nitrogen, maintaining cellular pH, detoxification of the cells, and scavenging of free radicals are proposed functions for these compounds under stress conditions. NCC accumulation is usually correlated with plant salt tolerance, even though this correlation is based on untested hypotheses.

Additional key words: amides, imino acids, polyamines, proline, proteins, quaternary ammonium compounds.

Introduction

Nitrogen is present abundantly in the atmosphere. Few plants with the symbiotic bacteria and actinomycetes are able to use it. Atmospheric N_2 can also be used by plants after reduction to NH_3 by soil microorganisms. Organic nitrogen which originates from the microbial decomposition of plant and animal materials is often present in the soil in the form of amino acids (Glass and Siddiqi 1995). Inorganic nitrogen is present in the soil in plant available forms NO_3^- and NH_4^+. NH_4^+ also arises from industrial burning, volcanic activity, and forest fires, while NO_3^- arises from oxidation of N_2 by O_2 or ozone in the presence of ultraviolet radiation.

Nitrogen metabolism is complex and varies with species. In general, the first steps in the assimilation of nitrate is its reduction by the enzyme nitrate reductase to nitrite and then by nitrite reductase to NH_4^+. The nitrite and NH_4^+, however, are toxic. NH_4^+ is, therefore, rapidly converted to amide group of glutamine, glutamate and sometimes of asparagine or other amino acids.

Plants are subjected to salinity when they are grown on saline soil or irrigated with saline or brackish water. Predominant anions are Cl^-, SO_4^{2-}, NO_3^- and HCO_3- and cations Na^+, Ca^{2+}, Mg^{2+} and K^+. Salinity stress adversely affects plant growth and metabolism through osmotic effect of salts, nutritional imbalance and/or toxic ion effects. Plants may counteract the salinity by accumulating inorganic and/or organic solutes (Wyn Jones 1981, Gorham *et al.* 1985). This ensures continuous water absorption and pressure potential sufficient for growth (Maas and Nieman 1978). Inorganic ions are accumulated in the vacuole and organic osmolytes in the cytoplasm to balance vacuolar osmotic potential (Maas and Nieman 1978, Wyn Jones 1981, Gorham *et al.* 1985). They to be changed to organic solutes are termed compatible (nontoxic) osmolytes. Strogonov (1964), Strogonov *et al.* (1972) and Wyn Jones (1984) argued, however, that not all organic solutes accumulated under saline conditions have a positive value, *e.g.*, synthesis of certain amines in some stressed tissues enhanced salt toxicity. Among organic osmolytes that accumulate in plants grown in saline environment soluble nitrogenous compounds, organic acids, sugars and polyols are dominant (Gorham *et al.* 1981, 1986, Rains 1989, Fathi-Ettai and Prat 1990, Rhodes and Hanson 1993, Hanson

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Abbreviations: GB - glycinebetaine; HPS - heat shock proteins; NCC - nitrogen containing compounds; PA - polyamines; Pro - proline; Put - putrescine, QAC - quaternary amonium compounds; Spd - spermidine; Spm - spermine.

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et al. 1994, Ashraf 1994, Venkatesan and Chellappan 1998). This review will be, however, limited to discussion of the different nitrogen containing compounds (NCC) that frequently accumulated in plants subjected to salinity. These NCC include amino acids, amides, imino acids, betains and polyamines (PA). Proteins are also found to be increased under salt stress (Pareek *et al.* 1997, Hassanein 1999, Evers *et al.* 1999). In addition to osmoprotective and osmotic adjustment function which is usually suggested for the NCC, protection of cellular macromolecules, storage form of nitrogen, maintaining cellular pH, detoxification of the cells, and scavenging of free radicals are other proposed functions for these compounds under salinity stress (Kaur-Sawhney and Galston 1979, Yancey *et al.* 1982, Slocum *et al.* 1984, Drolet *et al.* 1986, Rabe 1990, Rhodes and Hanson 1993, Dubey 1997, Mansour 1998). NCC need relatively law amounts of carbon (Jefferies and Rudmik 1984) which may be a limiting resource in plants in saline environment, because of stomatal closure which reduces the flux of CO_2 to the leaves. In this chapter, various NCC induced in saline environment and have significant role in salt tolerance or adaptation to salinity have been reviewed.

Nitrogen uptake and assimilation in saline environment

Saline environment is generally deficient in nitrogen (Amonkar and Karmarkar 1995) and in addition salinity interfers with NO_3^- uptake in many plant species which decreases NO_3^- content (Grattan and Grieve 1994, Khan and Srivastava 1998). The reduction in NO_3^- uptake could be due mostly to high Cl^- content in saline soil. Addition of N to plants subjected to salinity improved their growth and yield and thus their salt tolerance (Dubey and Pessarakli 1995). Application of Ca^{2+} also increased NO_3^- uptake under salt stress and this may be attributed to Ca^{2+} involvement in maintaining membrane integrity or increased activity of NO_3^- transporter by Ca^{2+} in saline environment (Dubey 1997). Since NCC are accumulated despite NO_3^- reduction in many species in response to salinity stress (Munns and Termaat 1986), N in salt stressed plants may not be limiting.

Salinity altered the activities of NO_3^- assimilation enzymes; nitrate reductase, nitrite reductase, glutamine synthatase and glutamate synthase. The activity of nitrate reductase decreased in salt sensitive and increased in salt tolerant crop species and halophytes (Amonkar and Karmarkar 1995, Dubey 1997, Khan and Srivastava 1998). The activity of nitrite reductase was either inhibited or unaffected in many crop species and halophytes since this enzyme is generally less sensitive to salinity than nitrate reductase (Amonkar and Karmarkar 1995, Dubey 1997). Salinity increased or decreased the activity of glutamine synthase and glutamate synthase depending on species and their sensitivity to salinity. Higher activities of both enzymes are usually found in salt tolerant species and halophytes. In many plants, salinity increased the activity of glutamate dehydrogenase (another pathway for ammonia assimilation) showing that these plants may have the potential to assimilate NH_3 by this enzyme in saline environment (Amonkar and Karmarkar 1995, Dubey 1997).

Nitrogen regulation of phytohormones and acclimation to salinity

Nitrogen nutrition may affect plant response to salinity stress indirectly through alteration of endogenous phytohormones contents. Cytokinins are significant for salt-stressed plants (Ben-Ziobi *et al.* 1967, Kabar 1987, Stark 1997) since they have been shown to alleviate the salinity-induced growth inhibition (Amzallag 1997). For example, higher cytokinin content was found in nitrate treated plants compared with those receiving either ammonia or mixed nitrogen nutrition (Griffith and Banowetz 1995 and references cited therein). Kinetin supplied to salt-stressed plants diminished the symptomes of salinity stress in various plants (Ben-Zioni *et al.* 1967, Itai *et al.* 1968, Kabar 1987, Amzallag 1997). Phytohormones, modulated by nitrogen nutrition, may also affect plant response to saline environment through their effects on endogenous polyamines. Cytokinins can influence PA synthesis (Griffith and Banowetz 1995) and PA may have protective function under salt stress.

Modulation of salt tolerance by NCC

Amino acids are one form of NCC which have been shown to accumulate in glycophytes and in halophytes under salinity (Wyn Jones 1981, Rains 1989, Fathi-Ettai and Prat 1990, Dubey and Pessarakli 1995, Amonkar and Karmarkar 1995). These amino acids include Pro, arginine, alanine, glycine, serine, leucine, and valine. Non-protein amino acids, citrulline and ornithine, also accumulate in plants under stress (Rabe 1990). Among increased amino acids, Pro accumulates in larger amounts compared with other amino acids and in many plant species a remarkable increase in Pro content was observed (*e.g.* Wyn Jones *et al.* 1981, Rains 1989, Heuer 1994, Ashraf 1994, Dubey 1997, Ali *et al.* 1999). Phosphorylation of glutamate to glutamyl phosphate by the enzyme glutamate kinase is the first step in Pro biosynthesis. Glutamyl phosphate is then reduced to glutamate semialdehyde by semialdehyde dehydrogenase. Spontaneous cyclization of glutamate semialdehyde gives pyrroline-5-carboxylate which is reduced by pyrroline-5-carboxylate reductase to give Pro (Singh 1995). Increased accumulation of amino acids in stressed plants could be caused by *1*) protein degradation (Becker and Fock 1986), *2*) inhibition of protein synthesis (Dhindsa and Cleland 1975), *3*) decreases in amino acids and amide export (Tully *et al.* 1979), *4*) growth inhibition of leaves (Davies and van Volkenburgh 1983). Stress-induced protein degradation may be essential in providing amino acids for synthesis of new proteins suited for growth or survival under the modified conditions and also substrates for energy metabolism (Raymond *et al.* 1994). Plants vary greatly in their capacity to accumulate Pro or other amino acids under salinity. When plants subjected to salt stress, salt tolerant species/genotypes accumulate more free amino acids, particularly Pro, than sensitive ones (Wyn Jones *et al.* 1984, Heuer 1994, Dubey and Rani 1995, Dubey 1997, Ashraf 1997). Contents of free amino acids and Pro increased also during cell adaptation *in vitro* in cultures treated with NaCl (Hasegawa *et al.* 1986).

Salt treatment of crop species increased activity of the Pro biosynthetic enzyme pyrroline-5-carboxylate reductase and decreased activity of Pro oxidase (Ashraf 1994). Bacterial genes, engineered into plants and resulting in Pro overproduction can increase ability to tolerate salinity (Tarczynsky *et al.* 1993, Kishor 1995). Exogenous application of Pro was found to enhance growth of plants subjected to salt stress (Lone *et al.* 1987, Shaddad 1990). In some species, however, both salt tolerant and sensitive genotypes have similar concentrations of Pro and other free amino acids (Rains 1989), and even negative correlation between Pro content and salt tolerance has been shown (*e.g.* in soybean and blackgram by Moftah and Michel 1987, Ashraf 1989, Ashraf 1994). Small changes in concentration of total free amino acids have been observed in salt stressed sorghum (Weimberg *et al.* 1984). Accumulation of Pro was found not only in saline conditions but also under other environmental stresses suggesting that Pro accumulation is a non-specific response to salinity but rather an universal stress response (Ashraf 1997). In some cases, drought sensitive cultivars accumulate more Pro and other amino acids than tolerant cultivars during osmotic stress (Hanson and Hitz 1982, Galiba *et al.* 1989) and the authors considered this response as a sign of the drought injury and not as adaptation. It is also suggested that Pro has no adaptive role and may be a symptomic stress. Correlation between Pro content and solute potential in the presence or absence of osmotic stress has been observed, suggesting that Pro accumulation does not initiate salinity adaptation but it may be synthesized as a result of the initiation of other responses to salinity (Hasegawa *et al.* 1986). Because of the controversial data of Pro accumulation in genotypes differing in salt tolerance, Ashraf (1994) and Wyn Jones (1981) argued that Pro is not a plausible selection criterion for salt tolerance.

Pro as well as other amino acids accumulated under stress conditions have been mainly recognized as osmotic adjustment agents. They lower the cell osmotic potential to allow water absorption despite decreased soil water potential. Pro as well as other amino acids, even at high concentrations, do not interfer or inhibit the enzyme activities (Wyn Jones 1981, Wyn Jones *et al.* 1984, Ford 1984, Dubey 1997, Ashraf 1997). Some enzymes (*e.g.*, pyruvate kinase, lactate dehydrogenase) are perturbed, however, by arginine or lysine suggesting that not all amino acids are compatible solutes (Yancey *et al.* 1982). Pro has been also considered a nitrogen storing agent (Rains 1989). This is because in stressed plants Pro can be easily converted to glutamate which is involved in synthesis of other essential amino acids (Ashraf 1997). Pro can also stabilize membranes (Wyn Jones *et al.* 1984, Rudolph *et al.* 1986, Rains 1989, Hanson and Burnet 1994, Mansour 1998, Gadallah 1999). Mansour (1998) provides direct evidence that Pro can protect cell membrane against salt injury. NaCl-induced cellular aberrations in onion epidermis, resulting from cell membrane disruption, were mitigated by Pro application. A decrease in shoot Cl^- and Na^+ accumulation and thus enhanced growth in saline environment in response to exogenous Pro application was proposed to the effect of Pro on membrane stabilization (Lone *et al.* 1987).

Amides and imino acids: Amides like glutamine and asparagine (Fig. 1) were found to accumulate in salt stressed plants (Amonkar and Karmarkar 1995, Dubey 1997). They accumulate also under drought stress (Raggi 1994). Accumulation of asparagine was greater than of Pro in *Agrostis stolonifera* exposed to salt stress (Dubey 1997). The content of these amides is, however, relatively lower than other NCC. Imino acids, pipecolic acid and 5-hydroxypipecolic acid (Fig. 1) have been also shown to accumulate in plants subjected to salinity stress (Stewart and Larher 1980, Amonkar and Karmarkar 1995, Dubey 1997). They can also serve in osmotic adjustment. Protection of the intracellular macromolecules by these compounds can also be predicted (see Yancey *et al.* 1982).

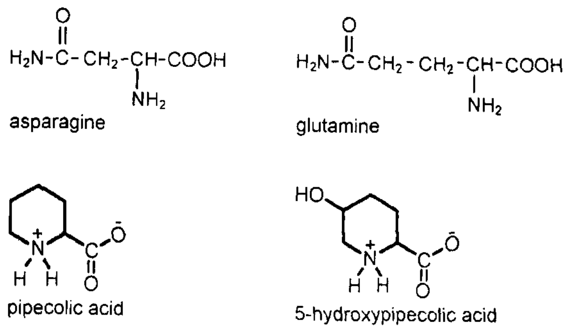

Fig. 1. Amides and imino acids that accumulate in plants under salinity stress.

Proteins: Although protein biosynthesis generally declines under stress conditions, cells preferentially synthesize specific stress proteins. Several proteins induced in response to saline environment have been identified from many plant species (Singh *et al.* 1985, 1987b, Hurkman *et al.* 1989, Ramagopal and Carr 1991, Pareek *et al.* 1997, Roy and Gurjar 1997, Ali *et al.* 1999). The authors differentiate two types of these proteins: those which accumulate in response to salt stress (salt stress proteins), and those which accumulate in response to a number of different biotic or abiotic stresses (stress-associated proteins). For example, heat shock protein (HSP 90) accumulates in response to heat shock, pathogen infection, cold, drought, and salt stress (Pareek *et al.* 1997). Similarly, accumulation of osmotin has been correlated to increased salt tolerance in plants (Singh *et al.* 1987b, LaRose *et al.* 1989), however, osmotin also accumulates in response to various stresses (Kononowicz *et al.* 1994). Proteins accumulated under salt stress may be synthesized *de novo* in response to salt, or may be present constitutively at low levels and are increased after salt exposure (Pareek *et al.* 1997). The higher content of some salt-induced proteins in salt tolerant than in salt sensitive rice and barley cultivars was observed (Rains 1989, Hurkman *et al.* 1989, Pareek *et al.* 1997). Pareek *et al.* (1997) suggest that stress proteins could be used as molecular markers and for genetic engineering experiments for improving salt tolerance in plants. Structural or membrane proteins (*e.g.* ATPases) have also been increased in several plant species grown in saline conditions. An increased activity of ATPases is critical for ion compartmentation under salinity stress. Also, Na^+/H^+ antiporters of tonoplast have been found to increase in sugar beet when grown under NaCl salinity (Garbarino and Dupont 1989, DuPont 1992). G-proteins and protein kinases, are supposed to be involved in signal traslocation between initial stimulus and activation of Na^+/H^+ antiporters (DuPont 1992). Proteins that accumulate in plants subjected to salinity may provide a storage form of nitrogen which is suitable for recycling nitrogen after relief of stress (Singh *et al.* 1987a) and may be involved in osmotic adjustment. A cross between two salt sensitive wheat cultivars and highly salt tolerant *Elytrigia elongata* produced two cultivars tolerant to high NaCl. However, salt stress affected twice as many genes in one cultivar than in the other suggesting that a number of genes which are affected by salt stress may have little or nothing to do with the control of salt tolerance (Roy and Gurjar 1997). Therefore, not all proteins produced in saline conditions are correlated with stress tolerance.

Quarternary ammonium compounds: The abundant QAC that accumulate in plants under salinity stress include glycinebetaine, β-alaninebetaine, Probetaine, hydroxyprolinebetaine and pipecolatebetaine (Fig. 2). For reviews see Wyn Jones and Storey (1981) and Rhodes and Hanson (1993). Among these compounds, glycinebetaine (GB) accumulates in largest amount in plants exposed to salinity (Wyn Jones and Storey 1981, Wyn Jones 1984, Rhodes and Hanson 1993, Hanson and Burnet 1994, Hanson *et al.* 1994, Venkatesan and Chellappan 1998). GB occurs in at least 11 families including monocotyledons and dicotyledons whereas some other QAC accumulate only in halophytes (*e.g.* β-alaninebetaine; Hanson and Burnet 1994).

There is near linear correlation between leaf osmotic potential and GB, β-alaninebetaine, and prolinebetaine content in several plant species (Grieve and Maas 1984, Rhodes and Hanson 1993). Accumulation of GB under salt stress was found to be high in salt tolerant grasses (Hitz and Hanson 1980, Wyn Jones and Storey 1981, Grieve and Maas 1984, Hanson and Grumet 1985), whereas salt sensitive grasses exhibited a low capacity for GB acumulation (Storey *et al.* 1977, Hitz and Hanson 1980, Rhodes *et al.* 1987). GB is synthesized by a two-step oxidation of choline, via the intermediate betainealdehyde. Also, the activity of GB synthesizing enzymes (*e.g.*, betaine aldehydehydrogenase) was increased in several plant species at high NaCl concentration (Weigel *et al.* 1986, McCue and Hanson 1990). Exogenous application of GB enhanced growth of crop plants under different stresses (Itai and Paleg 1982, Lone *et al.* 1987, Zhao *et al.* 1992). Addition of choline, GB precursor, to the growth medium increases acclimation of salt sensitive wheat genotype to NaCl stress (Mansour *et al.* 1993). Transgenic barley (Ishitani *et al.* 1995) and tobacco (Holmstrom *et al.* 1994) which overproduce GB show enhanced tolerance to stress. No correlation between GB accumulation and salt tolerance has been found in wheat (Wyn Jones *et al.* 1984). GB does not accumulate in many important crop species, such as tomato, potato, rice, carrot and sorghum (Weimberg *et al.* 1984, Fallon and Philips 1989, McCue and Hanson 1990). Therefore, evidence is not sufficient that GB is causatively related to plant salt tolerance (Wyn Jones 1980).

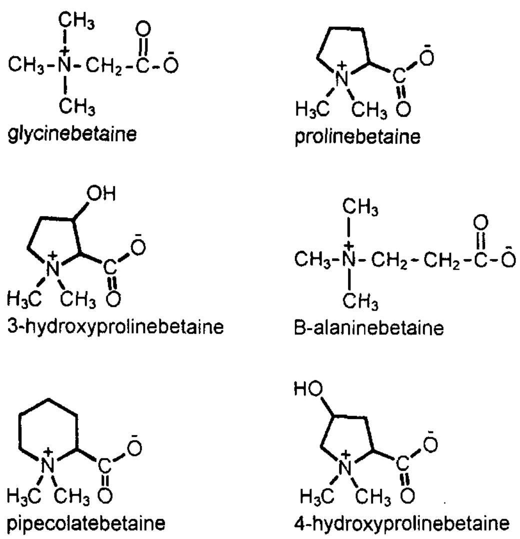

Fig. 2. Abundant quaternary amnonium compounds of higher plants that accumulate under salinity stress.

QAC are involved in osmotic adjustment under different stresses (Wyn Jones and Storey 1981, Low 1984, Wyn Jones *et al.* 1984, Rhodes and Hanson 1993, Khan *et al.* 1998) and GB confers enzyme and membrane protection under various conditions (Pollard and Wyn Jones 1979, Nash *et al.* 1982, Jolivet *et al.* 1982, Coughlan and Heber 1983, Jolivet *et al* 1983, Rhodes and Hanson 1993, Hanson and Burnet 1994, Mansour 1998, Gadallah 1999). GB is mainly localized in chloroplasts (Rhodes and Hanson 1993) and its accumulation contributes to chloroplast adjustment and protection of thylakoid membrane thus maintaining photosynthetic activity (Robinson and Jones 1986, Genard *et al.* 1991). GB application increased net photosynthetic rate of salt stressed tomato and turnip which was due to increased stomatal conductance and decreased photorespiration (Maleka *et al.* 1999).

Polyamines: The most common polyamines in higher plants include diamine putrescine (Put), triamine spermidine (Spd) and tetramine spermine (Spm). The diamines, diaminopropane and cadaverine are less common (Fig. 3). PA are classified as plant growth substances (Evans and Malmberg 1989), although their contents in plant cells are generally higher than those of plant hormones.

NaCl stress increased the content of Put and Spd in tobacco and rice (Shevyakova *et al.* 1985, 1994, Basu *et al.* 1988, Katiyer and Dubey 1990). In contrast, an increase in Put and decrease in Spd and Spm in rice cultivars grown under salt stress has been reported by Krishnamurthy and Bhagawat (1989). They also proposed that endogenous Put is involved in salt tolerance of rice. Accumulation of Put as a result of salinization was also observed in cotton and broad bean but not in sunflower or barley (Strogonov 1964, Strogonov *et al.* 1972). Put accumulation has been proposed to have adaptive value, as it serves as organic cation compensating partly for K in K deficient plants (Katiyer and Dubey 1990).

Exogenous application of PA was found to overcome the inhibitory effects of salinity in several species (Prakash and Prathapsanen 1988, Krishnamurthy 1991, Gadallah 1999). This leads Slocum *et al.* (1984) to suggest that PA may have a practical use in agriculture. The accumulation of PAs was, however, higher in salt sensitive than in salt tolerant calli of sugar beet (Le Dily et al. 1991) and in rice (Katiyer and Dubey 1990). Similarly, Put content was higher in drought sensitive wheat cultivar relative to resistant one during osmotic stress (Galiba *et al.* 1989). Changes in PA contents have been reported in response to various kinds of stresses (Slocum *et al.* 1984, Kakkar and Rai 1997) which suggests that PA accumulation is a non-specific response to salinity.

$H_2N-(CH_2)_3-NH_2$
diaminopropane

$H_2N-(CH_2)_4-NH_2$
putrescine

$H_2N-(CH_2)_5-NH_2$
cadaverine

$H_2N-(CH_2)_4-NH(CH_2)_3-NH_2$
spermidine

$H_2N-(CH_2)_3-HN(CH_2)_4-NH(CH_2)_3-NH_2$
spermine

Fig. 3. Common and less common polyamines that accumulate in higher plants under salinity stress.

Various proposals have been advanced, however, to explain a physiological role for the accumulation of PA in saline conditions. As the PA can interact with the surface of membranes, by virtue of their polycationic nature, they can stabilize the membrane structure (Kaur-Sawhney and Glaston 1979, Slocum *et al.* 1984, Roberts *et al.* 1986, Kao 1995, Kakkar and Rai 1997, Mansour and Al-Mutawa 1999). PA can indirectly affect membrane binding enzymes because PA binding to membrane influences its fluidity (Slocum *et al.* 1984, Roberts *et al.* 1986). DiTomaso *et al.* (1989) presented, however, evidence to show that Put did not replace Ca^{2+} in maintaining membrane stability and such observation does not confirm the proposed role of PA in stabilizing membranes. Flores and Filner (1985) suggest that PA can act as a reserve of nitrogen so that plant can utilize it after relief of stress. Furthermore, PA may be involved in maintaining cellular pH and anion/cation balance. They could modulate enzyme activities and also play role in ammonia detoxification (Slocum *et al.* 1984, Flores 1990, Kakkar and Rai 1997). PA can also function as free radical scavengers (Dumbroff 1990). The contribution of PA in osmotic adjustment is minor relative to other nitrogenous compounds since their contents are not high enough to provide osmotic adjustment (Kakkar and Rai 1997). PA arise from amino acids through decarboxylation. As in mammalian cells and fungi, Put may be derived from ornithine by the enzyane ornithine decarboxylase. In higher plants, Put may be indirectly formed from arginine. Arginine is converted to agmatine utilizing the enzyme arginine decarboxylase. Agmatine then loses urea to form Put. Conversion of Put to Spd occurs by the enzyme spermidine synthase. Spd is converted to Spm by the action of the enzyme spermine synthase.

Conclusions and future prospects

Despite the vast amount of data that shows accumulation of NCC in plant species subjected to salinity stress, specific physiological and biochemical role of these compounds is still rather speculative. An attempt to provide unified hypothesis to explain the function of accumulation of NCC during stress conditions has been advanced by Rabe (1990): "stress conditions result in ammonia accumulation and nitrogenous compounds serve in detoxifying the cell ammonia". This may be, however, a plausible explanation for some stresses but does not necessarily apply to all stresses. For example, salt stress does not always lead to elevated endogenous ammonium content.

Considerable variations in accumulation of NCC have been shown among crop species differing in salt tolerance. NCC accumulate equally or even more in salt sensitive species/cultivars than in salt tolerant ones. Also, contradicting evidence concerning NCC involvement in adaptation mechanism under salt stress are shown. The information regarding NCC role in adaptation of plants to salt is, therefore, insufficient to warrant the conclusion that they may be associated with salt tolerance. This does not preclude, however, a significant role for NCC in salinity tolerance.

There are two important issues which need to be dealt with in future research in this area. Firstly, there is a need to obtain further detailed information about whether the changes in NCC during stress are part of acclimation mechanism which would improve stress tolerance, or are merely detrimental consequences of the environmental stress. Secondly, comprehensive and broad scale studies are required to elucidate conclusively the specific role of NCC in plant adaptation to salt stress. This is urgently important because understanding of the specific role of these compounds will definitely help our understanding of the physiological, biochemical and molecular basis of salt tolerance in plants. This will subsequently contribute to the first step towards the development of strategies for designing stress tolerant genotypes.

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