PHOTOSYNTHETICA 42 (4): 481-486, 2004

REVIEW

Effects of salt stress on basic processes of photosynthesis

P. SUDHIR and S.D.S. MURTHY*

Department of Biochemistry, Sri Venkateswara University, Tirupati-517 502, India

Abstract

Salt stress causes decrease in plant growth and productivity by disrupting physiological processes, especially photosynthesis. The accumulation of intracellular sodium ions at salt stress changes the ratio of K : Na, which seems to affect the bioenergetic processes of photosynthesis. Both multiple inhibitory effects of salt stress on photosynthesis and possible salt stress tolerance mechanisms in cyanobacteria and plants are reviewed.

Additional key words: carboxylases; carotenoids; chlorophyll; cyanobacteria; electron transport; eukaryotic algae; NaCl; photophosphorylation; photosynthetic rate; photosystems; phycobiliproteins; salt tolerance.

General introduction

Salt stress is a major abiotic stress problem in arid and semi-arid regions and irrigation areas. Approximately 7 % of the world's land area, 20 % of the world's cultivated land, and nearly half of the irrigated land is affected with high salt contents (Rhoades and Loveday 1990, Szabolcs 1994). High salt contents can influence physiological processes of both cyanobacteria and plants. Most plants are non-halophytes, with either a relatively low salt tolerance or severely inhibited growth at low salinity levels. Plant species differ awfully in the growth response to salinity (Batterton and Van Baalen 1971, Downton 1982, Moisender *et al.* 2002, Sheekh *et al.* 2002).

Salt stress affects plant physiology at both whole-plant and cellular levels through osmotic and ionic stress (Joset *et al.* 1996, Hayashi and Murata 1998, Hasegawa *et al.* 2000, Muranaka *et al.* 2002a,b, Ranjbarfordoei *et al.* 2002, Murphy *et al.* 2003). Osmotic stress is linked to salt stress: salt stress involves an excess of sodium ions whereas osmotic stress is primarily due to a deficit of water without a direct role of sodium ions (Hsiao 1986, Joset *et al.* 1996, Munns 2002). Ionic imbalance occurs in the cells due to excessive accumulation of Na^+ and Cl^- and reduces uptake of other mineral nutrients, such as K^+, Ca^{2+}, and Mn^{2+} (Ball *et al.* 1987, Hasegawa *et al.* 2000). The accumulation of toxic amounts of salts in the leaf apoplasm leads to dehydration and turgor loss, and death of leaf cells and tissues (Marschner 1995). Both the dehydration of cells and high sodium to potassium ratio due to accumulation of high amounts of sodium ions inactivate enzymes and affect metabolic processes in plants (Booth and Beardall 1991).

Salt stress has various effects on plant physiological processes such as increased respiration rate and ion toxicity, changes in plant growth, mineral distribution, membrane instability resulting from calcium displacement by sodium (Marschner 1986), membrane permeability (Gupta *et al.* 2002), and decreased efficiency of photosynthesis (Boyer 1976, Downton 1977, Kirst 1989, Hasegawa *et al.* 2000, Munns 2002, Ashraf and Shahbaz 2003, Kao *et al.* 2003, Sayed 2003). In this article we review the effects of salts stress on bioenergetic processes of photosynthesis.

Organization of photosynthetic electron transport system and function

Photosynthetic electron transport, a light-driven redox process involves the conversion of photon energy into the chemical energy. The site of photosynthetic electron transport is thylakoid membrane. In higher plants thylakoid membranes are located in the chloroplast, whereas in cyanobacteria these membranes are dispersed in the cytosol of intact cells. Four multi-protein complexes embedded in the thylakoid membranes are involved in the electron transport process: photosystem 2 (PS2), cytochrome (Cyt) b_6/f, photosystem 1 (PS1), and ATP synthase complex. In addition to these, two mobile electron carriers, namely plastoquinone (PQ) and plastocyanin (PCy), are also involved in this electron transport. Both photosystems (PS1 and PS2) are pigment-protein complexes.

Received 8 March 2004, *accepted* 5 October 2004.

*Corresponding author; fax: 91-8574-2248496, e-mail: sdsmurthy@lycos.com

PS2 primarily mediates non-cyclic electron transport from water to PQ. PS2 contains chlorophyll (Chl), pheophytin (Pheo), β-carotene, P680, quinone acceptors (Q_A and Q_B), and several intrinsic and extrinsic proteins of water oxidation complex. These electrons transfer from PQ pool to the cytochrome (Cyt) b_6/f complex. PS1 contains Chl *a*, P700, β-carotene, and several intrinsic and extrinsic polypeptides. P700 in PS1 enables it to pick up electrons from the Cyt b_6/f complex by way of PCy and raise them to a sufficiently high redox potential that, after passing through ferredoxin, can reduce $NADP^+$ to NADPH. The use of artificial electron donors, acceptors, and inhibitors has led to understanding the functions of chloroplasts. The sites of action of commonly used donors, acceptors, and inhibitors are as follows (compiled from Trebst 1974 and Murthy and Rajagopal 1995):

$$\mathrm{H_2O} \xrightarrow{\text{in1}} \mathrm{Z} \rightarrow \mathrm{P_{680}} \rightarrow \underset{\uparrow \text{d1}}{\mathrm{Pheo}} \rightarrow \overset{\overset{\text{a1}}{\uparrow}}{\mathrm{Q_A}} \xrightarrow{\text{in2}} \overset{\overset{\text{a2}}{\uparrow}}{\mathrm{Q_B}} \rightarrow \underset{\uparrow \text{d2}}{\mathrm{PQ}} \xrightarrow{\text{in3}} \underset{\uparrow \text{d3}}{\mathrm{Cyt}\ b_6f} \rightarrow \mathrm{PCy} \xrightarrow{\text{in4}} \mathrm{P_{700}} \rightarrow \overset{\overset{\text{a3}}{\uparrow}}{\mathrm{X}} \xrightarrow{\text{in5}} \mathrm{NADH^+}$$

where acceptors are a1: silicomolybdic acid; a2: phenylenediamine, p-benzoquinone, 2,5-dimethyl-p-benzoquinone, and 2,5-dichloro-p-benzoquinone; a3: methylviologen, anthraquinone, ferricyanide. Donors are d1: catechol, ascorbate, H_2O_2, diphenylcarbazide, NH_2OH; d2: duroquinol; d3: diaminodurene; dichlorophenolindophenol, tetramethyl phenyldurene. All are reduced by ascorbate. Inhibitors are in1: NH_2OH; in2: diuron; in3: dibromothymoquinone; in4: KCN and $HgCl_2$; in5: DSPD.

Salt stress effects on photosynthesis

Photosynthetic pigments: In higher plants, Chl content decreases in salt susceptible plants such as tomato (Lapina and Popov 1970), potato (Abdullah and Ahmed 1990), pea (Hamada and El-Enany 1994), and *Phaseolus vulgaris* (Seemann and Critchley 1985). But Chl content has been increased in salt tolerant plants such as pearl millet (Reddy and Vora 1986), mustard (Singh *et al.* 1990), and wheat (Kulshreshtha *et al.* 1987). Content of carotenoids (Cars) increased in rice plants under salt stress (Misra *et al.* 1997) and decreased in black cumin (Hajar *et al.* 1996).

Similarly, various response of Chl content to salt stress was found in some cyanobacteria. In *Synechocystis* sp. PCC 6803, at moderate (342 mM) NaCl concentration the Chl *a* content increased while at 684 or 1 026 mM it sharply decreased (Schubert and Hagemann 1990, Schubert *et al.* 1993). However, no change in Chl *a* content was observed in *Spirulina platensis* grown under 0.8 M NaCl (Verma and Mohanty 2000a, Lu and Vonshak 2002). In *Synechocystis* sp. PCC 6803, Schubert *et al.* (1993) found an increase in Cars content in response to high salinity (1 026 mM NaCl), namely in echinenone, oscillaxanthin, and myxoxanthophyll, while β-carotene showed only small differences. This increased Car content might diminish the amount of photons available for the absorption by Chl *a* by shadowing and thus, irradiance can act as secondary stress factor.

In cyanobacteria, phycobiliproteins (PBPs) that are attached to the stromal surface of thylakoid membranes serve as the primary light-harvesting antenna for PS2. The composition and function of PBPs in cyanobacteria changed in response to stress conditions (Grossman *et al.* 1993). Salt stress mainly decreases the content of phycocyanin and thereby interrupts the energy transfer from PBPs to PS2 reaction centre (Schubert and Hagemann 1990, Schubert *et al.* 1993, Lu *et al.* 1999, Lu and Vonshak 2002). Sodium stress due to the addition of NaCl, $NaNO_3$, and $NaHCO_3$ caused decrease in the energy transfer from allophycocyanin to PS2 in *Sp. platensis* (Verma and Mohanty 2000b).

Photosynthetic electron transport reactions: Salt stress increases the accumulation of NaCl in chloroplasts of higher plants or in the cytoplasm of cyanobacterial cells, affects growth rate, and is often associated with decrease in photosynthetic electron transport activities in photosynthesis (Boyer 1976, Kirst 1989). In higher plants, salt stress inhibits PS2 activity (Mishra *et al.* 1991, Masojídek and Hall 1992, Belkhodja *et al.* 1994, Everard *et al.* 1994, Singh and Dubey 1995, Tiwari *et al.* 1997, Kao *et al.* 2003, Parida *et al.* 2003). In some studies salt stress had no effect on PS2 (Robinson *et al.* 1983, Brugnoli and Björkman 1992, Morales *et al.* 1992). The PS2 inhibition under salt stress was characterized by Misra *et al.* (1999). In some reports, the PS2 activity was decreased in response to salt stress due to the dissociation of 23 kDa polypeptide extrinsically bound to PS2 (Kuwabara and Murata 1982, Miyao and Murata 1983, Murata *et al.* 1992).

In cyanobacteria, various salt stress conditions stimulate the rate of respiration (Jeanjean *et al.* 1993, Lu and Vonshak 1999) and PS1 activity (Joset *et al.* 1996), and impair the rate of photosynthesis (Vonshak *et al.* 1988, 1995, Zeng and Vonshak 1998). Salt stress inhibited PS2 mediated oxygen evolution activity in *Synechocystis* sp. PCC 6803 (Schubert and Hagemann 1990, Schubert *et al.* 1993). Allakhverdiev *et al.* (2000) showed that the changes in K/N ratio inactivated both PS2 and PS1 in *Synechococcus* cells. Restoration of PS2 activity by diphenylcarbazide (DPC), an artificial electron donor to PS2 in salt treated cyanobacterial thylakoids, suggests that water splitting complex is the site of action of salt stress in *Synechococcus* cells (Allakhverdiev *et al.* 2000). However, in some cyanobacteria the PS2 reaction centre is the target for salt stress. Depending on the environment, both the water oxidation complex and PS2 reaction centres (increase in the number of Q_B non-reducing sites) are targets for salt stress in *S. platensis* (Lu *et al.* 1999, Lu and Vonshak 2002). Recently, Allakhverdiev *et al.* (2002) reported for *Synechocystis* that the combination of light and salt stress inactivated PS2 activity; particularly, salt stress inhibited the *de novo* synthesis of proteins, specifically the synthesis of D1 protein of PS2.

In cyanobacteria and eukaryotic algae, salt stress increased electron transport activity of PS1 (Gilmour *et al.* 1985, Canaani 1990, Fork and Herbert 1993, Jeanjean *et al.* 1993, Endo *et al.* 1995, Hibino *et al.* 1996, Lu and Vonshak 1999). Upon a shift to high salt stress, the amount of P700 and PS1 reaction centres was increased in *Synechocystis* sp. PCC 6803 (Jeanjean *et al.* 1993). This in turn caused increase in the cyclic electron transport around PS1.

Photophosphorylation and CO_2 fixation: In cyanobacteria, salt stress increases the efficiency of photophosphorylation by stimulating the cyclic photosynthetic electron flow around PS1 (for review, see Joset *et al.* 1996). Upon the addition of high amount of NaCl to the growth medium the activity of cyclic photophosphorylation was increased in *Synechocystis* sp. PCC 6803 (Jeanjean *et al.* 1993). The first step of photosynthetic CO_2 assimilation is catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO; EC 4.1.1.39) in C_3 plants, and by phospho*enol*pyruvate carboxylase (PEPC; EC 4.1.1.31) in C_4 plants. Salt stress enhances the oxygenase activity of RuBPCO while it curtails its carboxylase activity (Sivakumar *et al.* 2000). In the halotolerant cyanobacterium *A. halophytica*, the content of RuBPCO and the rate of CO_2 fixation are increased in response to high salt stress (Takabe *et al.* 1988). Echevarría *et al.* (2001) and García-Mauriño *et al.* (2003) reveal that PEPC activity is enhanced by salt stress.

Importance of low NaCl in photosynthesis

The significance of sodium for cyanobacterial photosynthesis has been demonstrated in several cases including growth (Miller *et al.* 1984, Brown *et al.* 1990), nitrogen fixation (Apte and Thomas 1983, Maeso *et al.* 1987), the uptake of nutrients such as nitrate and phosphate (Rodriguez *et al.* 1988, Fernandez-Valiente and Avendano 1993), and energy transduction (Brown *et al.* 1990). Chiefly in cyanobacteria, a decrease in the cellular content of both Chl and PBPs (Maeso *et al.* 1987) was observed in the sodium deficient medium. The loss in photosynthetic net oxygen evolution was observed in S*ynechocystis* sp. PCC 6714 (Zhao and Brand 1989), in alkaliphilic cyanobacterium *S. platensis* (Schlesinger *et al.* 1996, Pogoryelov *et al.* 2003), and in alkali tolerant cyanobacterium *Synechocococcus leopoliensis* (Miller *et al.* 1984, Espie *et al.* 1988) upon the sodium deprivation from growth medium. The effect of loss in PS2 activity due to sodium deprivation is reversible by the addition of Ca^{2+} and Na^+ in *Synechocystis* (Zhao and Brand 1988, 1989). Na-ions are important in cyclic electron transport around PS1 under stress (Van Thor *et al.* 2000). A group of cyanobacteria living at alkaline pH require sodium to maintain acidic intracellular pH relative to the external alkaline pH which is maintained by Na^+/H^+ antiporter activity and thereby prevent the loss of all physiological and metabolic activities (Krulwich *et al.* 1982, Krulwhich 1995, Pogoryelov *et al.* 2003).

Tolerance mechanisms in response to salt stress

A variety of salt tolerance mechanisms observed in photosynthesising organisms is given below.

1. Higher plants are particularly limited in their salt tolerance range, whereas other photosynthetic organisms such as cyanobacteria acclimate better (Joset *et al.* 1996). Many plants and cyanobacteria exposed to salt stress produce co-solutes such as sucrose, trehalose, proline, glucosyl-glycerol, and glycine-/glutamate-betaine (Gorham *et al.* 1985, Nomura *et al.* 1995). These co-solutes play an important role in salt tolerance of plants and cyanobacteria (for review see Joset *et al.* 1996).

2. In plants, exogenous addition of proline protects plant growth and productivity by reducing the production of free radicals and/or scavenging the free radicals (Singh *et al.* 1996, Jain *et al.* 2001). Also the external supplements of Ca^{2+} ameliorate the effects of salinity in plants, most probably by facilitating higher K : Na selectivity (Miyao and Murata 1984, Hasegawa *et al.* 2000).

3. In *Synechocystis*, un-saturation of fatty acids in the thylakoid membranes is important for the tolerance of photosynthetic machinery to salt stress. Un-saturation of fatty acids reverses the suppressed activity and synthesis of the Na^+/H^+ antiporter system due to salt stress (Allakhverdiev *et al.* 1999).

4. Vacuolar H^+-ATPase is required for salt tolerance as it imports cations such as Na^+ into the vacuole (Golldack and Dietz 2001, Hamilton *et al.* 2002, Parks *et al.* 2002). In cyanobacteria, P-ATPase, which is located in the plasma membrane, is responsible for extrusion of Na^+ from cytoplasm (Peschek *et al.* 1994).

Conclusions

The above studies show that salt stress exhibits various inhibitory effects on bioenergetic processes of photosynthesis. For better understanding of the mechanisms of salt stress, comparative studies should be made using the salt stress resistant mutants. In-addition, studies made at molecular level would help understand the adaptive mechanisms and initiation of responses under salt stress.

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