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REVIEW

Photosynthesis and salinity: are these mutually exclusive?

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Abstract

Photosynthesis has walked into the path of evolution for over millions of years. Organisms relying directly on photosynthesis, when subjected to adverse environments for a long duration, experience retardation in their growth and development. Salinity stress is perceived as one of the major threats to agriculture as it can cause an irreversible damage to the photosynthetic apparatus at any developmental stage of the plant. However, halophytes, a special category of plants, carry out all life processes, including photosynthesis, without showing any compromise even under high saline environments. The fascinating mechanism for Na^+ exclusion from cytosol besides retaining photosynthetic efficiency in halophytes can provide a valuable genetic resource for improving salt stress tolerance in glycophytes. Understanding how plants stabilize their photosynthetic machinery and maintain the carbon balance under saline conditions can be extremely useful in designing crops for saline and dry lands.

Additional key words: adaptation; chlorophyll; glycophytes; halophytes; photosynthesis; salinity.

Introduction

The most accepted theory of evolution by Oparin-Haldane hypothesized that the early cells, evolved during the highly reduced primitive atmosphere on the Earth, were simple heterotrophic cells. These unicellular organisms survived on organic compounds present at the ocean floor. As organic matter begun to deplete due to a highly reduced environment (and organic material was not synthesized), cells gradually evolved from being heterotroph to autotroph. This change enabled the cells to use either chemical compounds or sunlight to synthesize organic material for food (Stanley 1973, Lazcano and Miller 1996).

Plants, as sessile autotrophic organisms, are capable of harvesting light energy and converting it into chemical energy, which is used later as the carbon source. The process of synthesis of carbohydrates by green plants or pigmented organisms by utilizing carbon dioxide and water with the release of oxygen, in the presence of sunlight, is called 'photosynthesis'. This process of light harvesting directly or indirectly supports all living organisms on the Earth. Significance and relevance of photosynthesis to the scientific community is obvious as ten Nobel Prizes pertaining to this research area have been awarded so far (Fig. 1). Thus, owing to the fundamental nature of this process, it is imperative to understand the basics of this 'physico-bio-chemical' event to ensure food security. It is estimated that human population on the Earth is going to cross 9.1 billion by the year 2050 and by the same time, the land available for agriculture in developed countries is going to be reduced by 50 million hectares (http://www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/ How_to_Feed_the_World_in_2050.pdf).

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Abbreviations: CAM – Crassulacean acid metabolism; CBB – Calvin–Benson–Bassham cycle; CP – chloroplast protrusions; GB – glycine betaine; G3P – glyceraldehyde-3-phosphate; PA – polyamines; 3PGA – 3-phosphoglycerate; PEP – phospho*enol*pyruvate; PRC – photochemical reaction centre; PTOX – plastid terminal oxidase; Put – putrescine; RC – reaction centre; RuBP – ribulose-1,5-bisphosphate; SQDG – sulphoquinovosyldiacylglycerol; Spm – spermine; Spd – spermidine.
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This situation warrants a thorough understanding of the process of photosynthesis to ensure enough food production by crop plants. The present review is targeted to highlight the basic discoveries of the process as well as the recent reports pertaining to the study of photosynthesis, as influenced by salinity.

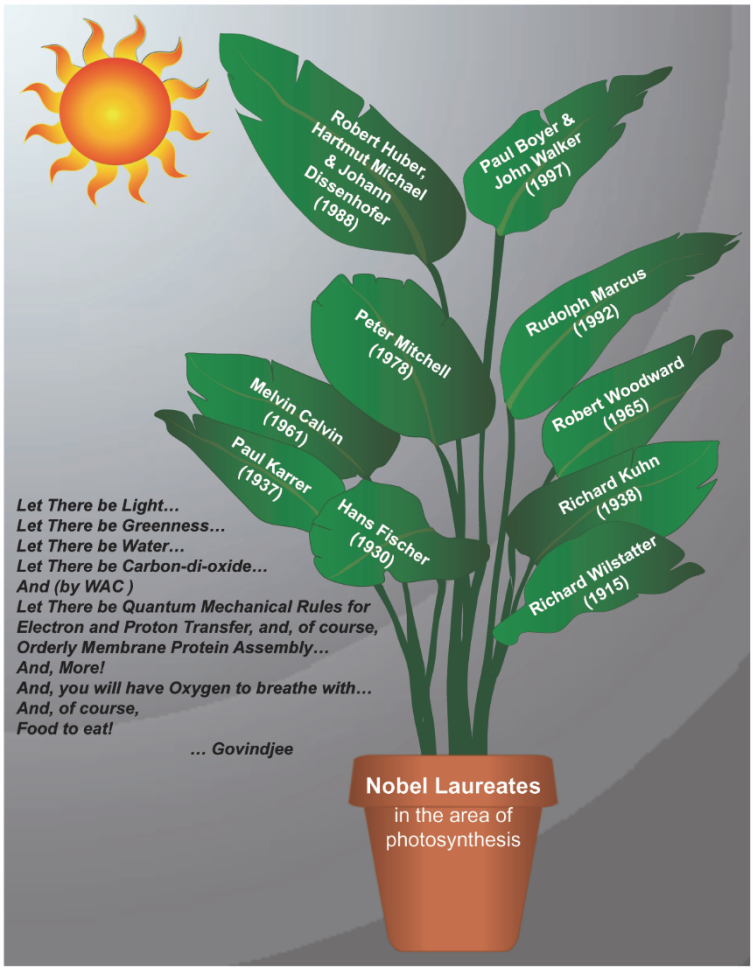

Fig. 1. Schematic representation depicting the significant contributions of the Nobel laureates from the field of photosynthesis. Richard Willstatter (1915): purified chlorophyll *a* and *b*. Hans Fischer (1930): synthesized hemin identified the molecular structure of porphyrin. Paul Karrer (1937): elucidated the chemical structure of carotenoids, vitamin A, and C. Richard Kuhn (1938): discovered α, β, and γ-carotene. Melvin Calvin (1961): traced the path of CO_2 (Calvin–Benson–Bassham cycle). Robert Woodword (1965): synthesized chlorophyll along with quinine, cholesterol, cephalosporin, and colchicine. Peter Mitchell (1978): discovered the chemiosmotic mechanism of ATP synthesis. Rudolph Marcus (1992): formulated the rate of electron transfer reactions (Marcus theory). Robert Huber, Hartmut Michael, and Johann Dissenhofer (1988): crystallized light-harvesting complex and reaction centre from *Rhodobacter*. Paul Delos Boyer, John Ernest Walker and Jens Christian Skou (1997): discovered ATP synthase, an enzyme responsible for ATP synthesis. The poem by Professor Govindjee aptly describes the importance of photosynthesis in every sphere of life.

Photosynthesis: From basics to application

The word 'photosynthesis', as coined by Charles R. Barnes in 1893, came much later into practice since the process was actually discovered. Even though the information on who was the pioneer of discovering the process of photosynthesis is very vague (as many scientists were involved), the timeline of discoveries in this area is represented in Fig. 1S (*supplement available online*). In this figure, the leading discoveries starting from the simple pot experiment done by Jan B.V. Helmont (1648) till Ravindra Kale and co-workers (2017) finding that both hydroxyl radical ($HO^{\bullet}$) and superoxide ($O_2^{\bullet-}$) damage the PSII during photoinhibition have been placed in a chronological manner (Thomas *et al.* 2002, Govindjee *et al.* 2003, Govindjee *et al.* 2004, Krogmann and Govindjee 2004, Kale *et al.* 2017). The time period spanning between 1648 till present have engaged several scientists passing the baton of photosynthesis research. Yet, research in this area has not come to an end and is likely not going to end

soon. Unfolding the molecules and elements involved in this process has now led us to an era when scientists are working towards improving the photosynthetic efficiency of crops for a better yield (http://c4rice.irri.org/; http://www.agprofessional.com/news/rice-being-genetically-modified-C3-c4-plant).

Physico-bio-chemistry of photosynthesis

In a biological system, the process of photosynthesis requires several physical elements, such as light, water, and air, performing the chemistry of converting light energy into chemical energy.

Photosynthetic reaction centre

The primary reaction of photosynthesis begins with a photochemical reaction, where light is absorbed by the well-arranged pigment antenna molecules (light-harvesting complex molecules) followed by a series of electron-energy transfers. This primary reaction takes place in the photosystem units present in the thylakoid membrane of the chloroplast. The antenna molecules comprising of chlorophyll (Chl) *a*, Chl *b*, β-carotenoids, zeaxanthin, *etc*., are arranged in such a way that they can absorb maximum photons of light at a given time. Illumination of antenna molecules, leading to its excitement, is followed by transfer of a electron to the well arranged protein-pigment molecule complex known as the photochemical reaction centre (PRC) or reaction centre (RC) (reviewed by Senge *et al*. 2014). The arrangement of RC is organism specific. It is in this reaction centre that light energy is converted into chemical energy (Allen and Williams 1998, Ben-Shem *et al.* 2003). On the basis of electron acceptor molecules, reaction centres are classified as: iron-sulfur type and pheophytin-quinone type (Allen and Williams 1998, Senge *et al.* 2014). Higher plants have two types of reaction centre complexes working together in a sequence wherein, one of the reduced photoreceptor (PSII) acts as an electron donor to the PSI molecule. The two photosystems are linked by cytochromes and other electron acceptor molecules. PSII consists of a membrane protein complex of 700 kDa size and catalyzes the photolysis of water (Suga *et al.* 2015). The loss of the electron from PSII is compensated by photolysis of water molecule (Arnon 1971). Some anoxygenic bacteria such as green sulfur bacteria have only PSI (Allen and Williams 1998, Senge *et al.* 2014), which consists of 14 subunits having an average of 200 light-harvesting pigment molecules (Ben-Shem *et al.* 2003). The flow of electrons from the donor to the acceptor with subsequent release of energy is termed as electron transport chain reaction (Senge *et al.* 2014, Shevela *et al.* 2017).

Chl pigments play a crucial role in harvesting the light energy. Five different forms of Chl have been identified, Chl *a, b, c, d*, and *f* (reviewed by Willows *et al.* 2013). Organisms can absorb diverse wavelengths of light due to the presence of these different forms of Chl (Thomas *et al.* 2002). Chl consists of a heterocyclic chlorin ring derived form pyrrol with a little variation on their side chain. Any alteration in the side chain by either substitution or addition can lead to change in light absorbance. It also has magnesium tetrapyrrole that functions in light capturing and transferring excitation energy to the reaction centres, which further drive the charge separation reaction in the reaction centres (Thomas 1967, Chen 2014).

Two phases of photosynthesis in plants

Photosynthetic reactions are traditionally divided into two phases. The first light-dependent phase takes place in the thylakoid membrane of the chloroplast. As light energy reaches the reaction centre *via* the light-harvesting complex, it excites the electron present in the pigment Chl (P_{700}) of PSII. The oxidized P_{700} gets reduced and release an electron, which further undergoes a downhill process called electron transport chain reaction. Transfer of electron in the electron transport chain flows in a "Z" pattern, therefore, it is also commonly known as Z-scheme model (downhill) of electron transport (Hill and Bendall 1960, Thomas *et al.* 2002, Yamori and Shikanai 2016). It is estimated that there are roughly twenty intermediate molecules involved in the Z-scheme of electron transport chain reaction (reviewed by Mohapatra and Singh 2015). Every step in the electron transport chain lowers the energy of the excited electron which gets harnessed into another form of energy, *i.e.,* ATP and NADPH. Meanwhile, as mentioned earlier, the electrons lost by the Chl pigment (P_{700}) of PSII is generated back by splitting of water molecules into half molecule of oxygen, an electron and a proton in PSII. The oxygen produced is released from the stomata of the leaf (Arnon 1971, Vinyard *et al.* 2013, Shevela *et al.* 2017). Comprehensive schematic diagram of the Z-scheme of oxidative photosynthesis is illustrated by Govindjee and Veit (2010) and is available freely for public learning in http://www.life.illinois.edu/govindjee/Z-Scheme.html.

The second light-independent phase takes place in the stroma of the chloroplast. It is in this process that CO_2 is fixed by the plants to make food. Several byproducts and enzymes, such as ribulose-1,5-bisphosphate (RuBP), 3-phosphoglycerate (3PGA), glyceraldehyde-3-phosphate (G3P), 1,3-bisphosphoglycerate, RuBP carboxylase/

oxygenase (Rubisco), transketolase, and epimerase, are involved in this process. The reaction is a cyclic process consisting of 11 steps wherein, RuBP undergoes a series of redox changes, which is later regenerated again for the cycle to continue. This process is broadly divided into three major steps; the first step, which is the carbon fixation step, is the process where RuBP (a five-carbon molecule) assimilates CO_2 with the help of the enzyme Rubisco. The addition of CO_2 onto RuBP gives rise two stable molecules with three carbons, *i.e.,* 3PGA. Further, 3PGA is phosphorylated and gets reduced to G3P (reduction step) which is the precursor for carbohydrates. These first two steps, *i.e.,* the carbon fixation and reduction steps, are driven by ATP and NADPH generated during the electron transport chain of the light reaction phase of photosynthesis. In the final regeneration step, G3P after undergoing a series of carbon shunting regenerates back to RuBP (Bassham *et al.* 1950, Bassham 2003, Raines 2003, Hügler and Sievert 2011, Biel and Fomina 2015). The reaction cycle also known as Calvin-Benson-Bassham cycle (CBB cycle) in honor of the discoverers, namely, Melvin Calvin, James Bassham, and Andrew Benson from California University, Berkeley.

Diversity in photosynthesis process: Depending on the first stable carbon product, which is formed after CO_2 assimilation, plants are either called C_3 or C_4. In C_3 plants, CO_2 is assimilated directly by the process of CBB cycle forming 3PGA (Bassham *et al.* 1950). In this system, Rubisco undergoes two competitive enzymatic reactions, carboxylation (to fix CO_2) or oxygenation (to fix O_2). Fixing O_2 instead of CO_2 leads to the production of a two-carbon molecule, *i.e.,* phosphoglycolate. This wasteful photosynthetic reaction is termed as photorespiration, wherein phosphoglycolate further inhibits few photosynthetic enzymes. In order to further recycle the glycolate to glycerate, specifically in peroxisomes and mitochondria, energy in the form of ATP is consumed (Leegood 2007).

On the other hand, the light-independent reaction or dark reaction and CBB cycle or reproductive pentose phosphate cycle are spatially separated in C_4 carbon fixation or the Hatch-Slack pathway. The light-independent reaction occurs in mesophyll cells, whereas the CBB occurs in the bundle sheath cells. Fixation of CO_2 occurs in the mesophyll cells wherein, phospho*enol*-pyruvate carboxylase (PEPC) catalyzes the formation of a four carbonic acid molecule – oxaloacetate. Oxaloacetate, later on, is converted into malate by malate dehydrogenase that is further transported into the bundle sheath for CBB cycle. Due to the physical separation between the CO_2 fixation step and CBB cycle, photorespiration does not occur in these plant types (Williams *et al.* 2012).

Moreover, few xerophytic plants adopt another unique mode of carbon fixation called CAM pathway, which is a slightly modified form of C_4 cycle. In this process, CO_2 fixation and CBB cycles are separated temporally within the same cell type (De-Paoli *et al.* 2014). CO_2 fixation takes place during night in the mesophyll cells (when the stomata are open) and CBB cycle occurs during the day (Males and Griffiths 2017). This adaptation minimizes the photorespiration as well as transpiration. CAM plants display the highest water-use efficiency by using 20–80% less water to produce a similar amount of biomass as compared to C_4 or C_3 plants (von Caemmerer *et al.* 2012). The CAM pathway is relatively an unexploited area in agricultural research with only a few significant crops such as pineapple and agave (Fig. 2*A*) adopting this process (Sage 2014). CAM represents an example of a convergent physiological syndrome, having evolved independently across genera (Males and Griffiths 2017). Recently, pineapple genome sequencing revealed that CAM-pathway genes are enriched with *cis*-regulatory elements associated with their circadian regulation. In addition, pineapple CAM photosynthesis has been suggested to have evolved by reconfiguration and neofunctionalization of pre-existing C_3 genes (Ming *et al.* 2015).

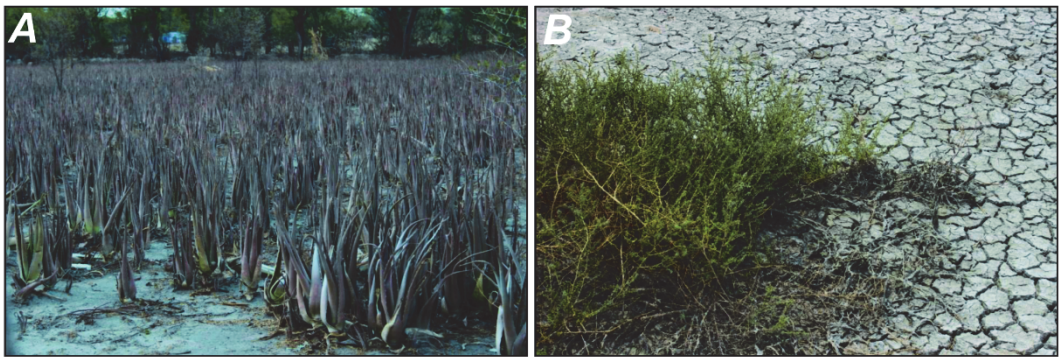

Fig. 2. Xerohalophytes are adapted to dry and saline conditions. Adaptation at molecular, anatomical, and physiological level enables them to carry out photosynthesis under such conditions. Shown here: (*A*) *Aloe vera* from a field in Rajasthan, India and (*B*) *Suaeda sp.* growing wild in Rajasthan, India.

Factors affecting photosynthesis: Several environmental factors ranging from biotic to abiotic stress adversely revegetate the process of photosynthesis. Some of the factors affecting photosynthesis in various plants are: excessive light intensity (Mano *et al.* 2016), low light intensity (Dong *et al.* 2014), duration of light (Takache *et al.* 2015), high temperature (Mathur *et al.* 2014), cold (Paredes and Quiles 2015), drought (Reddy *et al.* 2004), CO_2 concentration (Forkel *et al.* 2016), oxygen concentration (Busch and Sage 2017), water (Tezara *et al.* 1999), mineral/nutrient availability (Briat *et al.* 2015), air pollution (McLaughlin *et al.* 1982), heavy metals (Clijsters and Assche 1985), Chl content (Leverenz 1987), carbohydrate concentration accumulated in plants (Arp 1991), and salinity (Sultana *et al.* 1999). In this review, we focus specifically on salinity stress and its effect on photosynthesis of model plants, such as rice, wheat, maize, and *Arabidopsis*.

Photosynthesis is directly related to biomass and mass of a plant (Kebeish *et al.* 2007, de-Souza *et al.* 2008). About 10–40% of the energy goes directly into biomass accumulation under optimal conditions. Stress ultimately leads to reduced biomass accumulation (Munns and Gilliham 2015). Therefore, any change in the rate of photosynthesis is directly reflected on plant's biomass and growth. Brugnoli and Lauteri (1991) subjected cotton and beans to different salinity levels and observed that the dry mass of cotton was reduced up to 35% at 50 mM and by 60% at 250 mM NaCl. The effect was seen to be more severe in beans where the dry mass was reduced by 77% at 50 mM and 91% at 150 mM NaCl. Thus, it can be inferred that salinity causes a severe reduction in biomass accumulation (Joshi *et al.* 2016).

Salinity causes toxicity in plants

Salinity, a major abiotic stress, is the one that has led to the loss of more than 830 million hectares of arable land worldwide (Hoang et al. 2016). According to United Nations University Institute for Water, Environment and Health (UNU-INWEH) report (2014), about 20% of irrigated land (equivalent to the total area of France) and 2.1% of total dry land agriculture worldwide are affected by salinity. For the past 20 years, an average of 2,000 ha of irrigated agriculture land, both arid and semiarid, is being degraded due to salinity. From a period of two decades (1990–2010), it has been estimated that salinization has increased from 45 million ha to 62 million ha with an estimated loss of about 27 billion USD per annum (Qadir *et al.* 2014).

Salinity stress cause a physiological and metabolic imbalance in plants. Its effects disturb the vital steps of germination, development, photosynthesis, respiration, and ultimately leads to reduced crop yield (Purty *et al.* 2008, Kumari *et al.* 2009a, Joshi *et al.* 2016). Salinity stress causes a domino effect of stress comprising of osmotic and ionic stresses on plants. Firstly, plants sense a quick shock of osmotic stress (as the water potential of the soil becomes lower than the water potential of plants), resulting in a physiological drought condition. Secondly, the ions, such as Na^+ and Cl^-, which enter the plant, cause ionic imbalance and further hinder the uptake of minerals such as K^+, Ca^{2+}, and Mn^{2+} (Das *et al.* 2015a, Nongpiur *et al.* 2016, Ahmadizadeh *et al.* 2016). Excess of Na^+ in the leaves leads to sodium toxicity, resulting in marginal yellowing with progressive necrosis. The symptoms are similar to that of micronutrient toxicity. Chloride ions cause premature yellowing or bronzing of leaf tips and further cause necrosis of the leaf (Cassaniti *et al.* 2009). To prevent plants from necrosis, glycophytes either sequester excessive Na^+ ions into their vacuoles or exclude them out from the cell.

Salinity and photosynthesis

Salinity, as mentioned above, irrespective of its stage of occurrence, leads to a severe retardation in plant growth, development as well as yield. At the same time, photosynthesis is also essential for plants under salinity stress for survival. Thus, the question arises whether these two are mutually exclusive? Several studies in relation to photosynthesis and salinity have led to the understanding that plants generally respond to salinity by reducing the rate of photosynthesis (Brugnoli and Lauteri 1991, Tripathi *et al.* 2016, Joshi *et al.* 2017, Gupta *et al.* 2017). This occurs due to several molecular changes that are initiated physiologically and reflected morphologically (Fig. 3). Brief representations of the changes, which occur in plants due to salinity, are discussed below.

Morphological/anatomical changes: Salinity stress severely influences glycophytes with varying effects in different plant species. Under natural conditions, salinity level varies widely between dry and monsoon period and its effect comes with the combination of other stress elements. Poljakoff-Mayber (1975) found that humidity along with salinity causes severe growth retardation as compared to nonhumid environment. Under salinity, the stem diameter was found to be reduced due to shrinking of the vascular tissues, primarily the cortical parenchyma, secondary xylem and pith (Zhang *et al.* 2016). Salinity also causes succulence in the leaves of tomato and cotton (Strogonov 1964). Hayward and Long (1941) have shown that increasing the salt concentration thickens the area of

the lamina in tomato, while the thickness of spongy mesophyll and palisade layer decreases markedly. In contrast, the growth rate of bean leaves decreases immediately after salt stress, but its thickness increases due to increase in the size of spongy mesophyll layer and palisade layer (Meiri and Poljakoff-Mayber 1967). However, succulency was not observed in leaves of wheat and barley in response to salinity, indicating differential response in mono- and dicotyledonous plants under salinity (Strogonov 1964, Udovenko *et al.* 1970).

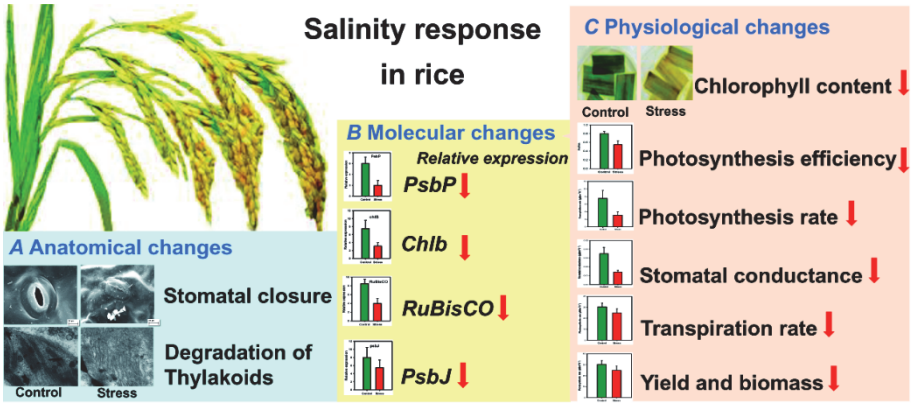

Fig. 3. Schematic diagram showing representative changes associated with the process of photosynthesis at an anatomical, molecular, and physiological level in glycophytes, such as rice, in response to salinity stress. In plants, changes at the anatomical level result in the closure of stomata and degradation of the thylakoid membrane. At the same time, cumulative molecular studies have established the influence of salinity in downregulating the genes involved in the process of photosynthesis such as PSII subunit P (*PsbP*), light-independent protochlorophyllide reductase (*chlB*), ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and PSII extrinsic subunit (*psbJ*). Change at the physiological level in glycophytes results in decrease in chlorophyll content, photosynthetic efficiency, photosynthetic rate, stomatal conductivity, and transpiration rate. The ultimate result of these changes is reflected by a decrease in the yield and biomass. Thorough understanding of these processes may contribute towards raising plants for dry and saline lands.
Supplementary Figure 1: Timeline depicting important developments in photosynthesis research.

It has been well established that salinity stress causes ultrastructural damage by altering the structure of cellular organelles, such as chloroplasts and mitochondria (Bastías *et al.* 2013). Salinity causes swelling and degradation of thylakoid and chloroplast envelope, and further increases the size and number of plastoglobuli. This ultimately causes disintegration of granal stacking (Pareek *et al.* 1997, Lee *et al.* 2013, Meng *et al.* 2016). The severity of salinity can be observed by analyzing the levels of organization of thylakoids, swelling of granal compartments inside the chloroplast. Damage in the thylakoid is caused primarily by the ROS produced in the leaves during salinity. High salinity in rice leads to several distortions of the chloroplast structure and also causes rolling of the lamellar system, accumulation of lipid droplets, and distinct "Hecht-fibres" between the plasmalemma and cell wall (von Willert and Kramer 1972). Salinity also causes a complete alteration in the thylakoid membrane protein structure. About 40% of D1 protein (a thylakoid membrane protein) is lost under salinity, which results in the inhibition of PSII activity (Sudhir *et al.* 2005). In *Cucumis sativus*, the microscopic study revealed that salinity causes damage to the chloroplast envelope. Due to aberrations in the thylakoid membrane, number of Chl molecules decreases whereas a number of plastoglobuli increases (Shu *et al.* 2012). Aberration of thylakoid membrane leading to disruption of grana stacking in rice is shown in Fig. 3*A*. Salinity stress also affects the ion-transporting membrane proteins in *Chenopodium album*. In contrast, the fatty acid composition of the chloroplastic membrane remains unaffected under salt stress (Ivanova *et al.* 2016). In rice, chloroplast protrusions (CPs) were observed under salinity stress. CPs consists of some of the denatured Rubisco which is transported to the cytoplasm and vacuole for degradation (Yamane *et al.* 2012). This was also confirmed by the presence of autophagy-related ATG8 protein in CPs, degradation of Rubisco (Ishida *et al.* 2008, Wada *et al.* 2009). The degradation of Rubisco is correlated with deformation of chloroplast ultrastructure, *i.e.,* transformation into gerontoplasts, characterized by disintegrated thylakoid membranes and numerous plastoglobuli (Krupinska 2006). In addition, the formation of Rubisco-containing body (RCB) in young and senescing leaves also characterizes chloroplast deformation (Prins *et al.* 2008).

Physiological changes: In response to salinity stress physiological changes can be immediately observed in plants, as the ionic imbalance triggers molecular signaling as a defense response. Sufficient knowledge about how salinity affects plants at the molecular levels is now available (Pareek *et al.* 2010, Nongpiur *et al.* 2012, Kumari *et al.* 2013, Nongpiur *et al.* 2016). However, plant breeders and biotechnologist face challenges in connecting these molecular changes to the changes in physiological responses (Chaves *et al.* 2009). Polyploids are more

heterozygous than their diploid counterparts with several redundant genes and evolutionary mechanisms to adapt towards adverse environments (Stebbins 1966). Allohexaploid wheat (*Triticum aestivum*) showed better salt tolerance than its tetraploid (*T. turgidum*) and diploid (*Aegilops tauschii*) progenitors (Farooq and Azam 2007, Yang *et al.* 2014). Similarly, we also demonstrated that amphidiploid *Brassica* species (*Brassica juncea*) is superior to its diploid relative (*Brassica nigra*) in term of growth, electrolyte leakage and proline accumulation under salinity stress (Purty *et al.* 2008, Kumar *et al.* 2009). Comparative transcriptome analysis of salinity stress responsive genes also revealed their higher transcript abundance in *B. juncea* (Sharma *et al*. 2015). In addition, tetraploid turnip (*Brassica rapa*) and black locust (*Robinia pseudoacacia*) also exhibited better salt tolerance than their corresponding diploids under high salt concentration (Meng *et al.* 2011, 2016).

Salinity affects physiological dynamics of photosynthesis by lowering carbon assimilation, as CO_2 diffusion into the chloroplast is restricted. This occurs because hyperosmotic stress leads to the closure of stomata to maintain the turgor pressure of water in the leaf (Chaves *et al.* 2009, Gupta and Huang 2014). To mitigate the stress and ionic imbalances, ROS is produced which further leads to stomatal closure (Das *et al.* 2015 a,b). PSI and PSII present in the reaction centre protein complex generates most of the ROS in the chloroplast under stress (Oukarroum *et al.* 2015). ROS acts as an important signal molecule up to certain threshold concentration, but, if the content exceeds the maximum threshold, it causes oxidative damage to protein, nucleic acid, and lipids (Schieber and Chandel 2014). Salinity also reduces stomatal conductivity, carotenoid and Chl contents in bean, cotton (Brugnoli and Lauteri 1991), rice (Kumari *et al.* 2009b, Lakra *et al.* 2017), *Arabidopsis* (Yu and Assmann, 2016, Tripathi *et al.* 2016), tobacco (Shabala *et al.* 2007), barley (Liu *et al.* 2017), *etc*., which further impairs photosynthesis.

Electron transport chain of photosynthesis is severely affected by salinity. Oukarroum *et al.* (2015) subjected *Lemna gibba* plant to different salt concentrations to check its effect on photosynthesis. At high salinity (400 mM NaCl), PSI and PSII activity was inhibited, thus leading to disruption of electron transport chain. They found that the number of active PSII also decreased with increasing salinity. Chl *a* fluorescence also decreased which led to a decrease in the quantum yield (F_v/F_m) of PSII (Fig. 3*C*). This happens as salinity hinders the redox chemistry of Q_A which further slows down the transfer of the electron between Q_A and Q_B (Pospíšil 2009). Belkhodja *et al.* (1994) found that under high light and salinity, F_v/F_p ratio decreases drastically, whereas $(F_i - F_o)/F_v$ increases in barley. Delay in the electron transfer between the manganese complex and plastoquinone *via* Q_A and Q_B molecules leads to ROS formation, which is also known as the oxidative burst. This causes further damage to the PSII and hinders photosynthesis (Pospíšil 2009, Sharma *et al.* 2012, Oukarroum *et al.* 2015). In *Spirulina platensis*, only the activity of PSII and oxygen evolution was reduced, while PSI activity and the total amount of P_{700} increased under salinity (Negrão *et al.* 2017).

Similarly, Demetriou *et al.* (2007) reported that photosynthesis efficiency, functional size of antenna molecules, density of the active reaction centres, electron transport rate, nonphotochemical energy dissipation per active reaction centres, primary photochemical yield, performance index, structural and functional index, were severely inhibited in *Scenedesmus obliquus* (green algae) under salinity. In addition, under strong light intensity, the activity of PSII decreases and this phenomenon is known as photoinhibition. This happens as strong light leads to the production of ROS which in turn inhibits repair mechanism of PSII (Murata *et al.* 2007). Photoinhibition is enhanced under salinity as evident in rice (Porcel *et al.* 2015), *Dunaliella tertiolecta,* algae (Seepratoomrosh *et al.* 2016), diatoms (Juneau *et al.* 2015), *Chlamydomonas reinhardtii* (Neale and Melisa 1989), and maize (Samira *et al.* 2015).

Molecular changes: Several molecular signals lead to alteration in gene expression which further results in accumulation of stress-responsive proteins, secondary and primary metabolites as defense machinery under salinity have been well established. Several groups have worked earlier on identification and formulation of salinity stress responses at the molecular level (Deinlein *et al.* 2014, Golldack *et al.* 2014, Yoshida *et al.* 2014). Effect of salinity in rice seedlings has been studied extensively using proteomic approach (Pareek *et al.* 1995, 1998, Karan *et al.* 2009, Singh *et al*. 2012); a plethora of changes in protein abundance in response to salinity has been reported. Similarly, our group has worked on allele mining of salinity related genes, such as salt overly sensitive (SOS) (Purty *et al.* 2008, Kumar *et al.* 2009), histidine kinase (HKs) (Karan *et al.* 2009), and regulatory molecules, such as nucleosome assembly protein (NAP) histone family (Tripathi *et al.* 2016), mannose-1-phosphate guanyl transferase (Kumar R. *et al.* 2012), cyclophilin (Kumari *et al.* 2009a), glyoxalase (Singla-Pareek *et al.* 2008, Ghosh *et al.* 2014), histone-gene binding protein (Lakra *et al.* 2015), phosphoglycerate kinase-2 (Joshi *et al.* 2016), metallothioneins (Kumar G. *et al.* 2012), intermediate filament-like protein (Soda *et al.* 2016), *etc*., from rice, tobacco, and *Brassica* under salinity. These studies have unravelled several crucial regulatory nodes in salt stress-signaling network. A complex set of molecular cascades starting from 'perception' to the 'regulation of salinity-responsive genes' by plants has been well documented in research from our lab (Pareek *et al.* 2010, Nongpiur *et al.* 2012, Kumari *et al.* 2013, Nongpiur *et al.* 2016, Sharan *et al.* 2017).

With regard to photosynthesis, salinity specifically affects the molecular machinery in several ways. Salinity

leads to osmotic and water deficit stress, causing an increased accumulation of abscisic acid (ABA) in the shoots and roots (Gupta and Huang 2014). ABA primarily regulates the closure of stomata under stress (Jacob *et al.* 1999). A representation of stomatal closure of *Nepenthes* under stress obtained from scanning electron microscopy imaging is shown in Fig. 3*A*. However, exogenous ABA application causes rapid generation of H_2O_2, which further causes activation of Ca^{2+} channels, suppression of K^+ channels, and modulation of cytosolic pH of the guard cells (Wang and Song 2008). Expression as well as activity of Rubisco is also hindered under salinity. Spinach, when subjected to long-term salinity, shows a drastic decline in Rubisco content. It also hinders the uptake of Ca^{2+} and Mg^{2+} ions which decrease the membrane stability and Chl content (Delfine *et al.* 1998). Representation of the relative expression of Rubisco and Chl content in rice under salinity stress is shown in Fig. 3*B*. In *Amaranthus tricolor*, salinity leads to a decrease in Rubisco and Chl content whereas glycine betaine (GB) is accumulated abundantly (Wang and Nii 2000). GB is an osmoprotectant which helps in recovery of PSII from the photoinactive state (Athar *et al.* 2015).

Salinity, halophytes and photosynthesis

Halophytes represent 2% of the world's total flora. These species are widely distributed from normal soil to coastal regions, and highly saline and alkaline environments (Fig. 2*B*). These plants employ specific structural adaptations to alter physiological, biochemical, and molecular mechanisms to avoid toxic effects of Na^+ and Cl^- (Joshi *et al.* 2015, Zhang *et al.* 2016). Halophytes can provide possible clues for salt tolerance in glycophytes by exploiting their specific adaptive mechanisms (Volkov 2015). Salt tolerance in halophytes can be achieved either by salt exclusion or salt inclusion, which protect them from toxic effects of high salt content in the soil (Ashraf *et al.* 2006). In contrast to glycophytes, all halophytes accumulate high Na^+ ions whether grown in saline or nonsaline environments. This helps them in maintaining the shoot turgor using Na^+ as a cheap osmoticum (Shabala and Mackay 2011). *Tamarindus indica*, as well as *Sesuvium portulacastrum* were reported to accumulate the enormous amount of sodium within their shoots (Rabhi *et al.* 2009). Some halophytic species can even use Na^+ instead of K^+ to regulate turgor in their guard cells (Ozfidan-Konakci *et al*. 2016). However, most of the halophytes have a greater ability to retain K^+ in their mesophyll cells under increased apoplastic salinity to increase turgor pressure. Further limiting the uptake of Na^+ ions (Wu *et al.* 2013, Aslam *et al.* 2011). In Poaceae, salt tolerance is associated with enhanced selective uptake of K^+ over Na^+, thus maintaining high cellular K^+ contents under salt stress (Nawaz *et al.* 2014).

Salinity treatment has no effect on the water-use efficiency of some halophytes, such as in *Desmostachya bipinnata*. In addition, net photosynthetic rate, photosynthetic pigments, electron transport rate, and photochemical quenching also remained unaffected under moderate salinity (Asrar *et al.* 2017). In contrast, photosynthetic efficiency, CO_2 assimilation rate, and stomatal conductance were rather improved under salinity in few obligate halophytes, such as *Sesuvium portulacastrum* and *Tecticornia indica* (Rabhi *et al.* 2012). Salinity stress negatively affects photosynthesis in few halophytes as well, such as *Arthrocnemum perenne*, *Abutilon fruticosum*, and *Alternanthera bettzickiana* (Nieva *et al.* 1999). In *Suaeda fruticosa* (Fig. 2*B*), impairment of photosynthetic activity occurs due to a decrease in flow of electron transport chain to the quinone pool; while in *Halimione portulacoides,* this is due to high energy dissipation in PSII light-harvesting centres which lead to the production of ROS (Duarte *et al.* 2013). Similarly, in barley, high salt concentration affects lipid-synthesizing enzymes, such as galactosyltransferase and acylase, attached to the chloroplast envelope leading to decrease in galactolipid content of chloroplast membranes resulting in enhanced salt tolerance (Müller and Santarius 1978). Few key adaptations in the photosynthetic machinery of halophytes under salinity are presented in Table 1.

Halophytes also maintain higher net photosynthetic rate by stabilizing the photosystems to increase their efficiency (Bose *et al*. 2014). Sengupta and Majumder (2009) have shown that *Porteresia coarctata* (halophytic rice) and *Thinopyrum ponticum* (halophytic wheat) protect their photosynthetic machinery by enhancing the expression of Mn-stabilizing proteins of the oxygen-evolving complex in PSII, Chl *a-b* protein (CP47) involved in stabilization of the reaction centre protein D1 of PSII, PSI subunit IV protein essential for cross-linking ferredoxin-$NADP^+$ oxidoreductase, Rubisco large subunit, and Rubisco activase under salt stress. Similarly, *Thellungiella salsuginea* showed increased electron transport rate through PSII and plastid terminal oxidase (PTOX) protein in comparison to *Arabidopsis* during drought stress (Stepien and Johnson 2009). *Chenopodium quinoa* and *Carpobrotus rosii* also showed lower decrease in F_v/F_m in comparison to *Pisum sativum* and *Vicia faba* under salinity stress (Percey *et al.* 2016). Similarly, increase in sulpholipid content and modification of sulphoquinovosyldiacylglycerol (SQDG), known to protect PSII, was observed in *Aster tripolium* and *Sesuvium portulacastrum* (Ramani *et al.* 2004).

In addition, few C_3 (*Portulacaria afra* and *Mesembryanthemum crystallinum*) and C_4 (*Portulaca oleracea*) halophytes change their mode of carbon assimilation to CAM under salt stress to decrease salt-induced ROS production (Bose *et al*. 2014). *Atriplex lentiformis* showed a shift from C_3 to C_4 mode of carbon fixation in response

Table 1. Adaptations in halophytes enabling them to carry out photosynthesis under saline conditions.

Halophytes	Family	Mode of carbon assimilation	Salinity level	Effect on photosynthesis	Reference
Cakile maritima	Brassicaceae	C3	100 mM	Total pigments (chlorophyll, carotenoids, and anthocyanins), F_v/F_m, CO_2 assimilation, stomatal conductance (g_s) increased during vegetative stage stress	Debez *et al.* 2012
Suaeda fruticosa	Amaranthaceae	C3	300 mM	Genes related to photosystem such as PsbZ, psbD, psbC are up-regulated	Diray-Arce *et al.* 2015
Mesembryanthemum crystallinum	Aizoaceae	C3	500 mM	Under salinity, the plant adopt CAM photosynthetic pathway	Dyachenko *et al.* 2006
Salicornia brachiata	Amaranthaceae	C3	500 mM	High expression of Rubisco smaller subunit as well as Chl *a*/*b* binding protein	Jha *et al.* 2009
Plantago coronopus	Plantaginaceae	C3	25-100% sea water	Under high salinity, growth, stomatal conductance, net photosynthetic rate (P_N), water use efficiency (WUE) and leaf water potential decreases while carotenoid/ chlorophyll ratio and leaf area ratio (LAR) increases.	Koyro 2006
Pokkali (Oryza sativa)	Poaceae	C3	200 mM	High expression of Rubisco and PsbP genes contributes in maintaining photosynthesis	Lakra *et al.* 2017
Salvadora persica	Salvadoraceae	C3	250–1,000 mM	WUE, relative water content (RWC), P_N, g_s, transpiration rate (E), quantum yield of PSII (Φ_{PSII}), photochemical quenching (q_P), and electron transport rate (ETR) remained unaffected under low salinity, whereas these parameters reduced significantly under high salinity	Rangani *et al.* 2016
Nypa fruticans	Arecaceae	C3	300 mM	Chl *a*, Chl *b* and total chlorophyll remain unchanged	Theerawitaya *et al.* 2014
Suaeda splendens	Amaranthaceae	C4	400 mM	Shows highest level of photosynthetic efficiency (F_v/F_m) and WUE at 400 mM	Redondo-Gomez *et al.* 2008
Aeluropus lagopoides	Poaceae	C4	400 mM	Adapt salinity by increasing Mehler reaction with an increase in activity of PSII/CO_2	Moinuddin *et al.* 2017)
Aeluropus lagopoides	Poaceae	C4	450 mM	C4 photosynthesis protein such as alanine aminotransferase, aspartate aminotransferase and mitochondrial 2-oxoglutarate/malate translocator, chloroplast HSP70, chlorophyll a/b binding proteins were up-regulated under salinity	Sobhanian *et al.* 2010
Hordeum marinum	Poaceae	C4	300 mM	Two types of OEE proteins (OEE1 and OEE2) that are involved in the formation of OEC, which is a crucial component for PSII are accumulated. Thus maintained photolysis	Marsalova *et al.* 2016
Kandelia candel	Rhizophoraceae	C4	400 mM	High expression of PSI, PSII, Calvin cycle and chlorophyll binding related proteins	Wang *et al.* 2013
Panicum turgidum	Poaceae	C4	125 mM	High F_v/F_m followed by increased value of thermal energy dissipation (NPQ)	Koyro *et al.* 2013
Puccinellia tenuiflora	Poaceae	C4	450 mM	High accumulation of smaller subunit of RuBisCO, chlorophyll *a*/*b* binding protein and PSI reaction centre protein	Wang *et al.* 2007
Sesuvium portulacastrum	Aizoaceae	C4	300 mM	All photosynthetic elements such as pigments, proteins, *etc.*, are expressed abundantly at 300mM salinity	Yi *et al.* 2014
Thellungiella halophila	Brassicaceae	C4	400 mM	High accumulation of smaller subunit of RuBisCO and chlorophyll *a*/*b* binding protein	Zhang *et al.* 2008
Thellungiella salsuginea	Brassicaceae	C4	200 mM	Microarray analysis identified 52 and 41 unigenes involved in PSII and PSI respectively to be upregulated under abiotic stress.	Lee *et al.* 2013

to salinity stress (Meinzer and Zhu 1999). *Tecticornia indica* displayed Kranz anatomy with reduced leaves and fleshy stem cortex to avoid CO_2 leakage from the mesophyll to the atmosphere (Akhani *et al.* 1997). To overcome salinity stress, *S. fruticosa* increases its turgidity for salt dilution, while *H. portulacoides* develops an ionic compartmentalization strategy in the form of specific salt glands on the leaves to excrete the excess salt (Duarte *et al.* 2013). In *Atriplex patula*, succulence in leaf was observed due to an increase in epidermal and mesophyll thickness under salinity (Acosta-Motos *et al*. 2017). Similarly, for improving CO_2 diffusion and photosynthetic efficiency under salinity stress, *Myrtus communis* and *Eugenia myrtifolia* showed a remarkable increase in palisade parenchyma, while a decrease in spongy parenchyma was observed. Salt stress causes a negligible decrease in stomatal conductance of halophytes and their stomata remain open to fix CO_2 continuously (Shabala 2013). Thus, it is clear that different halophytes have evolved different structural and physiological modifications enabling them to carry out photosynthesis under extreme saline conditions and thus enabling their survival.

Approaches for analyzing photosynthesis-associated response in plants under salinity stress

Advanced technologies have led to extensive progress in understanding the complex pathways involved in enhanced stress tolerance in plants. However, these technologies further need to be improved for a better understanding of these tightly regulated and complex stress responses at the cellular level (Gupta *et al.* 2015). The omics-based technologies, such as transcriptomics, proteomics, and metabolomics, provide analysis and interpretation of the vast amount of data in a more precise manner (reviewed by Das *et al.* 2015a). This approach gives a complete framework of the molecular mechanism of an organism. The omics-based approach is more advantageous, as it allows one to study the genes in the whole genome (genomics), mRNAs (transcriptomics), proteins (proteomics), ions (ionomics), metabolites (metabolomics), *etc*., and integrate them together to systematically understand the complex approach of a system (Horgan and Kenny 2011, Soni *et al.* 2015). These techniques have been extensively used to study salinity and the process of photosynthesis, some of which are presented below.

Transcriptomics approach: Global transcriptome analysis using RNAseq to compare *Prochlorococcus* cells acclimated to different salt concentrations, *i.e.*, 3.8 and 5% (w/v) NaCl, showed a reduction in transcript abundance of genes involved in photosynthetic electron transport and cell division. In contrast, genes involved in carbon fixation, respiratory electron flow, osmolyte/compatible solute biosynthesis, and inorganic ion transport showed higher transcript abundance (Al-Hosani *et al.* 2015). Similarly, numerous studies have also shown the downregulation of PSI and PSII component genes, such as *psaB*, *psaL*, *psaK*, *psbT*, *psbB*, *psbJ*, and genes encoding Chl, such as *chlb*, *chlB*, *chlG*, *psaB*, and *psaA* under salt stress in rice (representation in Fig. 3*B*). Similarly, RNAseq of *Eleusine coracana* (finger millet) under salinity stress showed down-regulation of genes involved in photosynthesis, such as cytochrome b_6f complex iron-sulfur subunit, Chl *a*-*b* binding protein, and PSII core complex protein, such as triose phosphate isomerase, *psbY*, *etc*. (Rahman *et al.* 2014). Monitoring the expression of 7,000 full-length genes of *Arabidopsis* by cDNA microarray showed downregulation of 37 genes involved in photosynthesis, such as smaller subunit of ribulose-1,5-bisphosphate carboxylase, Chl *a*-*b* binding protein, and genes for components of PSI and PSII (Seki *et al.* 2002). Taken together, these studies clearly suggest the impairment of photosynthetic electron transport machinery under salt stress.

Proteomics approach: Proteomics deals with complete profiling of proteins to identify posttranslational modifications, degradation, mutation, polymorphism, and any changes in protein pattern during different stresses and conditions (Hernandez *et al.* 2006). Study of the proteome dynamics using pulse SILAC to check the photosynthesis response of *Chlamydomonas reinhardtii* (green algae) during the early stage of salt treatment showed drastic reduction in the synthesis of photosynthetic proteins, such as Rubisco, PSII protein units, and protein involved in CBB cycle, with increasing salt concentration (Mastrobuoni *et al.* 2012). Similarly, Neelam *et al.* (2013) analyzed the total thylakoid proteins of *C. reinhardtii* under salinity stress using blue native PAGE and found that several of the membrane proteins were downregulated due to altered protein–protein and protein–pigments interactions. Western blot using anti-PSII core protein and light-harvesting proteins of PSII (Lhcbs) showed that antennae protein molecules, such as CP47, CP43, and few other proteins such as Lhcb1 and Lhcb4, were down-regulated. Combined physiological and proteomics (using iTRAQ) analysis of cucumber (*Cucumis sativus* L.) leaves under salinity revealed that expression of photosynthesis proteins was altered under salinity. Proteins involved in CO_2 assimilation during CBB cycle, such as Rubisco, phosphoglycerate kinase, and subunit alpha, which binds the larger subunit of Rubisco, were downregulated. Whereas, proteins, such as glycerate dehydrogenase, peroxisomal (S)-2-hydroxy-acid oxidase, serine-glyoxylate aminotransferase, and glycine dehydrogenase, which are involved in photorespiration, were upregulated (Sang *et al.* 2016). Using 2D-PAGE, Thagela *et al.* (2017) analyzed the expression of proteins under salinity for *Azolla microphylla*. They found that proteins, such as glycine dehydrogenase, ATP-synthase, and chloroplastic protease,

which help in the normal functioning of photosynthesis, were downregulated. Of the 59 spots, which were found to be differentially expressed, most of the proteins were related to photosynthesis machinery and their reduced expression results in a decrease of biomass in *A. microphylla*. Proteomics analysis using SDS-PAGE reveals that the 47 kDa Chl protein (CP) and 94 kDa proteins were drastically reduced in *Spirulina* under salinity stress. This leads to the hindering of electron transfer from the antenna molecule to the PSII, which further changes the Chl fluorescence emission spectrum (Sudhir *et al.* 2005). Comparative proteomic analysis using DIGE for two contrasting rice genotypes, Pokkali and IR64, under different salinity stress showed that the content of proteins involved in light reaction centre, such as PsbP, and CBB cycle reaction protein, such as the large and small unit of Rubisco, were reduced drastically. But, the level of reduction is lower in Pokkali as compared to IR64, which is a salt-sensitive cultivar (Lakra *et al.* 2017).

Metabolomics approach: Salinity directly affects the metabolism of a plant by altering stomatal conductance, CO_2 assimilation, hampers electron transport chain, and also changes the level of stress-related gene expression. Response to the alteration of gene expression further leads to accumulation of osmolytes, such as sugars, proline, glycine betaine, polyamines, and glyoxalases, which help protect membrane stability (Chaves *et al.* 2009, Anwar *et al.* 2016, Gupta *et al.* 2017). Polyamines (PA), organic polycations, assist in various functions ranging from growth and development to adaptation during biotic and abiotic stress (Adiga and Prasad 1985). Spermine (Spm), spermidine (Spd), and putrescine (Put) are the most abundant and common PAs in plants. Under salinity stress, Put enhances the lipid accumulation in chloroplasts and thus prevent granal and thylakoid membrane degradation by its interaction with negatively charged membranes (Shu *et al.* 2012).

Conclusion: Photosynthesis directly contributes to the development and yield of plants. Any stress condition that hinders the photosynthesis activity in plants also results in adverse effects on its metabolism. Salinity directly inhibits photosynthesis by inhibiting stomatal opening, hindering CO_2 assimilation, obstructing electron transport chain, altering the expression of stress-related genes, *etc*. Therefore, to engineer salt-tolerant plants with reduced yield penalty, it is important to unravel key pathways regulating salt-response network. Combining together different 'OMICS' approaches could lead to the identification of probable routes for protection of the machinery associated with photosynthesis under salinity stress. Similarly, exploring halophytes at different ontogenic stages may assist in decoding the mechanism responsible for their ability to withstand photooxidative damage, water-use efficiency, and specialized adaptations to protect photosynthetic apparatus under saline conditions. In addition, halophytes can act as models to understand conservative growth strategies under high salinity and can act as genetic resources contributing towards the goal of improving salt tolerance in crops.

References

Acosta-Motos J.R., Ortuño M.F., Bernal-Vicente A.: Plant responses to salt stress: Adaptive mechanisms. − Agronomy **7**: 18, 2017.

Adiga P.R., Prasad G.L.: Biosynthesis and regulation of polyamines in higher plants. − In: Galston A.W., Smith T.A. (ed.): Polyamines in Plants. Pp. 3-24. Springer, Dordrecht 1985.

Ahmadizadeh M., Vispo N.A., Calapit-Palao C.D. *et al*.: Reproductive stage salinity tolerance in rice: a complex trait to phenotype. − Indian J. Plant Physi. **21**: 528-356, 2016

Akhani H., Trimborn P., Ziegler H.: Photosynthetic pathways in *Chenopodiaceae* from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. − Plant Syst. Evol. **206**: 187-221, 1997.

Al-Hosani S., Oudah M.M., Henschel A. *et al*.: Global transcriptome analysis of salt acclimated *Prochlorococcus* AS9601. − Microbiol. Res. **176**: 21-28, 2015.

Allen J.F., Williams J.C.: Photosynthesis reaction centres. − FEBS Lett. **438**: 5-9, 1998.

Anwar K., Lakra N., Singla-Pareek S.L. *et al*.: Investigating abiotic stress response machinery in plants: The metabolomic approaches. − In: Dagar J.C., Sharma P.C., Sharma D.K. *et al*. (ed.): Innovative Saline Agriculture. Pp. 303-319. Springer, New Delhi 2016.

Arnon D.I.: The light reactions of photosynthesis. − P. Natl. Acad. Sci. USA **69**: 2883-2892, 1971.

Arp W.J.: Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. − Plant Cell Environ. **14**: 869-875, 1991.

Ashraf M., Hameed M., Arshad M. *et al*.: Salt tolerance of some potential forage grasses from Cholistan desert of Pakistan. − In: Khan M.A., Weber D.J (ed.): Ecophysiol. High Salinity Tolerance Plants. Pp. 31-54. Springer, Dordrecht 2006.

Aslam R., Bostan N., Maria M. *et al*.: A critical review on halophytes: salt tolerant plants. − J. Med. Plants Res. **5**: 7108-18, 2011.

Asrar H., Hussain T., Hadi S.M. *et al*.: Salinity induced changes in light harvesting and carbon assimilating complexes of *Desmostachya bipinnata* (L.) Staph. – Environ. Exp. Bot. **135**: 86-95, 2017.

Athar H.U.R., Zafar Z.U., Ashraf M.: Glycinebetaine improved photosynthesis in canola under salt stress: evaluation of chlorophyll fluorescence parameters as potential indicators. − J. Agron. Crop Sci. **201**: 428-442, 2015.

Bassham J.A., Benson A.A., Calvin M.: The path of carbon in photosynthesis − J. Biol. Chem. **185**: 781-787, 1950.

Bassham J.A.: Mapping the carbon reduction cycle: a personal retrospective. − Photosynth. Res. **76**: 35-52, 2003.

Bastías E., González-Moro M.B., González-Murua C.: Interactive effects of excess boron and salinity on histological and ultrastructural leaves of *Zea mays* amylacea from the Lluta

Valley (Arica-Chile). − Cienc. Investig. Agrar. **40**: 581-595, 2013.

Belkhodja R., Morales F., Abadia A. *et al*.: Chlorophyll fluorescence as a possible tool for salinity tolerance screening in barley (*Hordeum vulgare* L.). − Plant Physiol. **104**: 667-673, 1994.

Ben-Shem A., Frolow F., Nelson N.: Crystal structure of plant photosystem I. − Nature. **426**: 630-635, 2003.

Biel K., Fomina, I.: Benson-Bassham-Calvin cycle contribution to the organic life on our planet. − Photosynthetica **53**: 161-167, 2015.

Bose J., Shabala L., Pottosin I. *et al*.: Kinetics of xylem loading, membrane potential maintenance, and sensitivity of K^+-permeable channels to reactive oxygen species: physiological traits that differentiate salinity tolerance between pea and barley. – Plant Cell Environ. **37**: 589-600, 2014

Briat J.F., Dubos C., Gaymard F.: Iron nutrition, biomass production, and plant product quality. − Trends Plant Sci. **20**: 33-40, 2015.

Brugnoli E., Lauteri M.: Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C3 non-halophytes. − Plant Physiol. **95**: 628-635, 1991.

Busch F.A., Sage R.F.: The sensitivity of photosynthesis to O_2 and CO_2 concentration identifies strong RuBisCO control above the thermal optimum. − New Phytol. **213**: 1036-1051, 2017.

Cassaniti C., Leonardi C., Flowers T.J.: The effects of sodium chloride on ornamental shrubs. − Sci. Hortic.-Amsterdam **122**: 586-593, 2009.

Chaves M.M., Flexas J., Pinheiro C.: Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. − Ann. Bot.-London **103**: 551-560, 2009.

Chen M.: Chlorophyll modifications and their spectral extension in oxygenic photosynthesis. − Annu. Rev. Biochem. **83**: 317-340, 2014.

Clijsters H., van Assche F.: Inhibition of photosynthesis by heavy metals. − Photosynth. Res. **7**: 31-40, 1985

Das P., Nutan K.K., Singla-Pareek S.L. *et al*.: Understanding salinity responses and adopting 'omics-based' approaches to generate salinity tolerant cultivars of rice. − Front. Plant Sci. **6**: 712, 2015a.

Das P., Nutan K.K., Singla-Pareek S.L. *et al*.: Oxidative environment and redox homeostasis in plants: dissecting out significant contribution of major cellular organelles. − Front. Environ. Sci. **2**: 70, 2015b.

Debez A., Braun H.P., Pich A. *et al*.: Proteomic and physiological responses of the halophyte *Cakile maritima* to moderate salinity at the germinative and vegetative stages. − J. Proteomics. **75**: 5667-5694, 2012.

Deinlein U., Stephan A.B., Horie T. *et al*.: Plant salt-tolerance mechanisms. − Trends Plant Sci. **19**: 371-379, 2014.

Delfine S., Alvino A., Zacchini M. *et al*.: Consequences of salt stress on conductance to CO_2 diffusion, RuBisCO characteristics and anatomy of spinach leaves. − Aust. J. Plant Physiol. **25**: 395-402, 1998.

Demetriou G., Neonaki C., Navakoudis E. *et al*.: Salt stress impact on the molecular structure and function of the photosynthetic apparatus-the protective role of polyamines. − BBA-Bioenergetics **1767**: 272-280, 2007.

De-Paoli H.C., Borland A.M., Tuskan G.A. *et al*.: Synthetic biology as it relates to CAM photosynthesis: challenges and opportunities. – J. Exp. Bot. **65**: 3381-3393, 2014.

De Souza A.P., Gaspar M., Da-Silva E.A. *et al*.: Elevated CO_2 increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. − Plant Cell Environ. **31**: 1116-1127, 2008.

Diray-Arce J., Clement M., Gul B. *et al*.: Transcriptome assembly, profiling and differential gene expression analysis of the halophyte *Suaeda fruticosa* provides insights into salt tolerance. − BMC Genomics **16**: 353, 2015.

Dong C., Fu Y., Liu G. *et al*.: Low light intensity effects on the growth, photosynthetic characteristics, antioxidant capacity, yield and quality of wheat (*Triticum aestivum* L.) at different growth stages in BLSS. − Adv. Space Res. **53**: 1557-1566, 2014.

Duarte B., Santos D., Marques J.C. *et al*.: Ecophysiological adaptations of two halophytes to salt stress: photosynthesis, PS II photochemistry and anti-oxidant feedback–implications for resilience in climate change. − Plant Physiol. Bioch. **67**: 178-188, 2013.

Dyachenko O.V., Zakharchenko N.S., Shevchuk T.V. *et al*.: Effect of hypermethylation of CCWGG sequences in DNA of *Mesembryanthemum crystallinum* plants on their adaptation to salt stress. − Biochemistry-Moscow+ **71**: 461-465, 2006.

Farooq S., Azam F.: A new allopolyploid wheat for stressed lands and poverty alleviation. − Field Crop Res. **100**: 369-373, 2007.

Fleming I.: Absolute configuration and the structure of chlorophyll. − Nature **216**: 151-152, 1967.

Forkel M., Carvalhais N., Rödenbeck C. *et al*.: Enhanced seasonal CO_2 exchange caused by amplified plant productivity in northern ecosystems. − Science **351**: 696-699, 2016.

Ghosh A., Pareek A., Sopory S.K. *et al*.: A glutathione responsive rice glyoxalase II, *OsGLYII-2*, functions in salinity adaptation by maintaining better photosynthesis efficiency and anti-oxidant pool. − Plant J. **80**: 93-105, 2014.

Golldack D., Li C., Mohan H. *et al*.: Tolerance to drought and salt stress in plants: Unraveling the signaling networks. − Front. Plant Sci. **5**: 151, 2014.

Govindjee, Allen J.F., Beatty J.T.: Celebrating the millennium: historical highlights of Photosynthesis research, Part 3. − Photosynth. Res. **80**: 1-13, 2004.

Govindjee, Beatty J.T., Gest H.: Celebrating the millennium: historical highlights of Photosynthesis research, Part 2. − Photosynth. Res. **76**: 1-11, 2003.

Govindjee, Krogmann D.: Discoveries in oxygenic photosynthesis (1727–2003): a perspective. − Photosynth. Res. **80**: 15-57, 2004.

Govindjee, Veit W.: The Z-scheme of electron transport in photosynthesis. http://www.life.illinois.edu/govindjee/Z-Scheme.html (accessed continuously since August 2010), 2010.

Gupta B., Huang B.: Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. − Int. J. Genom. **2014**: 701596, 2014.

Gupta B.K., Sahoo K.K., Ghosh A. *et al*.: Manipulation of glyoxalase pathway confers tolerance to multiple stresses in rice. − Plant Cell Environ. DOI: 10.1111/pce.12968, 2017.

Gupta B.K., Tripathi A.K., Joshi R. *et al*.: Designing climate-smart future crops employing signal transduction components. − In: Pandey G.K. (ed.): Elucidation of Abiotic Stress Signaling in Plants: Functional Genomics Perspectives, Vol 2. Pp. 393-413. Springer, New York 2015.

Hayward H.E., Long E.M.: Anatomical and physiological responses of the tomato to varying concentrations of sodium

chloride sodium sulphate, and nutrient solutions. − Bot. Gaz. **102**: 437-462, 1941.

Hernandez P., Müller M., Appel R.D.: Automated protein identification by tandem mass spectrometry: Issues and strategies. − Mass Spectrom. Rev. **25**: 235-254, 2006.

Hill R., Bendall F.: Function of the two cytochrome components in chloroplasts: A working hypothesis. − Nature **186**: 136-137, 1960.

Hoang T.M., Tran T.N., Nguyen T.K. *et al*.: Improvement of salinity stress tolerance in rice: challenges and opportunities. − Agronomy **6**: 54, 2016.

Horgan R.P., Kenny L.C.: SAC review: 'Omic' technologies: genomics, transcriptomics, proteomics and metabolomics. − Obstet. Gynecol. **13**: 189-195, 2011.

Hügler M., Sievert S.M.: Beyond the Calvin cycle: autotrophic carbon fixation in the ocean. − Annu. Rev. Mar. Sci. **3**: 261-89, 2011.

Ishida H., Yoshimoto K., Izumi M. *et al*.: Mobilization of RuBisCO and stroma-localized fluorescent proteins of chloroplasts to the vacuole by an ATG gene-dependent autophagic process. − Plant Physiol. **148**: 142-155, 2008.

Ivanova T.V., Maiorova O.V., Orlova Y.V. *et al*.: Cell ultrastructure and fatty acid composition of lipids in vegetative organs of *Chenopodium album* L. under salt stress conditions. − Russ. J. Plant Physl+ **63**: 763-775, 2016.

Jacob T., Ritchie S., Assmann S.M., Gilroy S.: Abscisic acid signal transduction in guard cells is mediated by phospholipase D activity. − P. Natl. Acad. Sci. USA **96**: 12192-12197, 1999.

Jha B. Agarwal P.K., Reddy P.S. *et al*.: Identification of salt-induced genes from *Salicornia brachiata*, an extreme halophyte through expressed sequence tags analysis. − Genes Genet. Syst. **84**: 111-120, 2009.

Joshi R., Karan R., Singla-Pareek S.L. *et al*.: Ectopic expression of Pokkali phosphoglycerate kinase-2 (*OsPGK2-P*) improves yield in tobacco plants under salinity stress. − Plant Cell Rep. **35**: 27-41, 2016.

Joshi R., Prashat R., Sharma P.C. *et al*.: Physiological characterization of gamma-ray induced mutant population of rice to facilitate biomass and yield improvement under salinity stress. − Ind. J. Plant Physiol. **21**: 545-555, 2016.

Joshi R., Ramanarao M.V., Bedre R. *et al*.: Salt adaptation mechanisms of halophytes: Improvement of salt tolerance in crop plants. − In: Pandey G.K. (ed.): Elucidation of Abiotic Stress Signaling in Plants: Functional Genomics Perspectives, vol 2. Pp. 243-280. Springer, New York 2015.

Joshi R., Sahoo K.K., Tripathi A.K. *et al*.: Knockdown of an inflorescence meristem-specific cytokinin oxidase–*OsCKX2* in rice reduces yield penalty under salinity stress condition. − Plant Cell Environ. DOI: 10.1111/pce.12947, 2017.

Juneau P., Barnett A., Méléder V. *et al*.: Combined effect of high light and high salinity on the regulation of photosynthesis in three diatom species belonging to the main growth forms of intertidal flat inhabiting microphytobenthos. − J. Exp. Mar. Biol. Ecol. **463**: 95-104, 2015.

Kale R., Hebert A.E., Frankel L.K. *et al*.: Amino acid oxidation of the D1 and D2 proteins by oxygen radicals during photoinhibition of Photosystem II. − P. Natl. Acad. Sci. USA **14**: 2988-2993, 2017.

Karan R., Singla-Pareek S.L., Pareek A.: Histidine kinase and response regulator genes as they relate to salinity tolerance in rice. − Funct. Integr. Genomic. **9**: 411-417, 2009.

Kebeish R., Niessen M., Thiruveedhi K. *et al*.: Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. − Nat. Biotechnol. **25**: 593-599, 2007.

Koyro H.W., Hussain T., Huchzermeyer B. *et al*.: Photosynthetic and growth responses of a perennial halophytic grass *Panicum turgidum* to increasing NaCl concentrations. − Environ. Exp. Bot. **91**: 22-29, 2013.

Koyro H.W.: Effect of salinity on growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus* (L.). − Environ. Exp. Bot. **56**: 136-146, 2006.

Krupinska K.: Fate and activities of plastids during leaf senescence. − In: Wise R.R., Hoober J.K. (ed.): The Structure and Function of Plastids. Pp. 433-449. Springer, Dordrecht 2006.

Kumar G., Kushwaha H.R., Panjabi-Sabharwal V. *et al*.: Clustered metallothionein genes are co-regulated in rice and ectopic expression of *OsMT1e-P* confers multiple abiotic stress tolerance in tobacco *via* ROS scavenging. − BMC Plant Biol. **12**: 107, 2012.

Kumar G., Purty R.S., Sharma M.P. *et al*.: Physiological responses among *Brassica* species under salinity stress show strong correlation with transcript abundance for SOS pathway-related genes. − J. Plant Physiol. **166**: 507-520, 2009.

Kumar R., Mustafiz A., Sahoo K.K. *et al*.: Functional screening of cDNA library from a salt tolerant rice genotype Pokkali identifies mannose-1-phosphate guanyl transferase gene (*OsMPG1*) as a key member of salinity stress response. − Plant Mol. Biol. **79**: 555-568, 2012.

Kumari S., Roy S., Singh P. *et al*.: Cyclophilins: proteins in search of function. − Plant Signal. Behav. **8**: e22734, 2013.

Kumari S., Sabharwal V.P.N., Kushwaha H.R. *et al*.: Transcriptome map for seedling stage specific salinity stress response indicates a specific set of genes as candidate for saline tolerance in *Oryza sativa* L. − Funct. Integr. Genom. **9**: 109-123, 2009b.

Kumari S., Singh P., Singla-Pareek S.L. *et al*.: Heterologous expression of a salinity and developmentally regulated rice cyclophilin gene (*OsCyp2*) in *E. coli* and *S. cerevisiae* confers tolerance towards multiple abiotic stresses. − Mol. Biotechnol. 42: 195-204, 2009a.

Lakra N., Kaur C., Anwar K. *et al*.: Proteomics of contrasting rice genotypes: Identification of potential targets for raising crops for saline environment. − Plant Cell Environ. DOI: 10.1111/pce.12946, 2017.

Lakra N., Nutan K.K., Das P. *et al*.: A nuclear-localized histone-gene binding protein from rice (*OsHBP1b*) functions in salinity and drought stress tolerance by maintaining chlorophyll content and improving the antioxidant machinery. − J. Plant Physiol. **176**: 36-46, 2015.

Lazcano A., Miller S.L.: The origin and early evolution of life: Prebiotic chemistry, the Pre-RNA world, and time. − Cell **85**: 793-798, 1996.

Lee M.H., Cho E.J., Wi S.G. *et al*.: Divergences in morphological changes and antioxidant responses in salt-tolerant and salt-sensitive rice seedlings after salt stress. − Plant Physiol. Bioch. **70**: 325-35, 2013.

Leegood R.C.: A welcome diversion from photorespiration. − Nat. Biotechnol. **25**: 539-540, 2007.

Leverenz J.W.: Chlorophyll content and the light response curve of shade-adapted conifer needles. − Physiol. Plantarum **71**: 20-29, 1987.

Liu X., Fan Y., Mak M. *et al*.: QTLs for stomatal and photosynthetic traits related to salinity tolerance in barley. − BMC Genomics. **18**: 9, 2017.

Males J, Griffiths H.: Stomatal biology of CAM plants. − Plant Physiol. **174**: 550-560, 2017.

Mano J., Endo T., Miyake C.: How do photosynthetic organisms manage light stress? A tribute to the late Professor Kozi Asada. − Plant Cell Physiol. **57**: 1351-1353, 2016.

Maršálová L., Vítámvás P., Hynek R. *et al*.: Proteomic response of *Hordeum vulgare* cv. Tadmor and *Hordeum marinum* to salinity stress: similarities and differences between a glycophyte and a halophyte. − Front. Plant Sci. **7**: 1154, 2016.

Mastrobuoni G, Irgang S, Pietzke M. *et al*.: Proteome dynamics and early salt stress response of the photosynthetic organism *Chlamydomonas reinhardtii*. − BMC Genomics **13**: 215, 2012

Mathur S., Agrawal D., Jajoo A.: Photosynthesis: response to high temperature stress. − J. Photoch. Photobio. B **137**: 116-126, 2014.

McLaughlin S.B., McConathy R.K., Duvick D. *et al*.: Effects of chronic air pollution stress on photosynthesis, carbon allocation, and growth of white Pine trees. − Forest Sci. **28**: 60-70, 1982.

Meinzer F.C., Zhu J.: Efficiency of C4 photosynthesis in *Atriplex lentiformis* under salinity stress. − Funct. Plant Biol. **26**: 79-86, 1999.

Meiri A., Poljakoff-Mayber A.: The effect of chlorine salinity on growth of bean leaves in thickness and in area. − Israel J. Bot. **16**: 115-123, 1967.

Meng F., Luo Q., Wang Q. *et al*.: Physiological and proteomic responses to salt stress in chloroplasts of diploid and tetraploid black locust (*Robinia pseudoacacia* L.). − Sci. Rep. **6**: 23098, 2016.

Meng H.B., Jiang S.S., Hua S.J. *et al*.: Comparison between a tetraploid turnip and its diploid progenitor (*Brassica rapa* L.): the adaptation to salinity stress. − Agr. Sci. China **10**: 363-375, 2011.

Ming R., VanBuren R., Wai C.M. *et al*.: The pineapple genome and the evolution of CAM photosynthesis. − Nat. Genet. **47**: 1435-1442, 2015.

Mohapatra P.K., Singh N.R.: Teaching the Z-Scheme of electron transport in photosynthesis: a perspective. − Photosynth. Res. **123**: 105-114, 2015.

Moinuddin M., Gulzar S., Hameed A. *et al*.: Differences in photosynthetic syndromes of four halophytic marsh grasses in Pakistan. − Photosynth. Res. **131**: 51-64, 2017.

Müller M., Santarius K.A.: Changes in chloroplast membrane lipids during adaptation of barley to extreme salinity. − Plant Physiol. **62**: 326-329, 1978.

Munns R., Gilliham M.: Salinity tolerance of crops – what is the cost? − New Phytol. **208**: 668-673, 2015.

Murata N., Takahashi S., Nishiyama Y. *et al*.: Photoinhibition of photosystem II under environmental stress. − BBA-Bioenergetics **1767**: 414-421, 2007.

Nawaz I., Iqbal M., Hakvoort H.W. *et al*.: Expression levels and promoter activities of candidate salt tolerance genes in halophytic and glycophytic *Brassicaceae*. − Environ. Exp. Bot. **99**: 59-66, 2014.

Neale P.J., Melis A.: Salinity-stress enhances photoinhibition of photosynthesis in *Chlamydomonas reinhardtii*. − J. Plant Physiol. **134**: 619-622, 1989.

Neelam S., Subramanyam R.: Alteration of photochemistry and protein degradation of photosystem II from *Chlamydomonas reinhardtii* under high salt grown cells. − J. Photoch. Photobio. B **124**: 63-70, 2013.

Negrão S., Schmöckel S.M., Tester M.: Evaluating physiological responses of plants to salinity stress. − Ann. Bot.-London **119**: 1-11, 2017.

Nieva F.J.J., Castellanos E.M., Figueroa M.E. *et al*.: Gas exchange and chlorophyll fluorescence of C3 and C4 saltmarsh species. − Photosynthetica **36**: 397-406, 1999.

Nongpiur R., Soni P., Karan R. *et al*.: Histidine kinases in plants: cross talk between hormone and stress responses. − Plant Signal. Behav. **7**: 1230-1237, 2012.

Nongpiur R.C., Singla-Pareek S.L., Pareek A.: Genomics approaches for improving salinity stress tolerance in crop plants. − Curr. Genomics **17**: 343-357, 2016.

Oukarroum A., Bussotti F., Goltsev V. *et al*.: Correlation between reactive oxygen species production and photochemistry of photosystems I and II in *Lemna gibba* L. plants under salt stress. − Environ. Exp. Bot. **109**: 80-88, 2015.

Ozfidan-Konakci C., Uzilday B., Ozgur R. *et al*.: Halophytes as a source of salt tolerance genes and mechanisms: a case study for the Salt Lake area, Turkey. − Funct. Plant Biol. **43**: 575-589, 2016.

Paredes M., Quiles M.J.: The effects of cold stress on photosynthesis in *Hibiscus* plants. − PLoS ONE **10**: e0137472, 2015.

Pareek A., Singla S.L., Grover A.: Immunological evidence for accumulation of two high-molecular-weight (104 and 90 kDa) HSPs in response to different stresses in rice and in response to high temperature stress in diverse plant genera. − Plant Mol. Biol. **29**: 293-301, 1995.

Pareek A., Singla-Pareek S.L., Grover A.: Proteins alterations associated with salinity, desiccation, high and low temperature stresses and abscisic acid application in seedlings of Pusa 169, a high-yielding rice (*Oryza sativa* L.) cultivar. − Curr. Sci. **75**: 1023-1035, 1998.

Pareek A., Singla S.L., Grover A.: Short-term salinity and high temperature stress-associated ultrastructural alterations in young leaf cells of *Oryza sativa* L. − Ann. Bot.-London **80**: 629-639, 1997.

Pareek A., Sopory S.K., Bohnert H.J. *et al*.: Abiotic Stress Adaptation in Plants. Pp. 526. Springer, Dordrecht 2010.

Percey W.J., McMinn A., Bose J. *et al*.: Salinity effects on chloroplast PSII performance in glycophytes and halophytes. − Funct. Plant Biol. **43**: 1003-1015, 2016.

Poljakoff-Mayber A.: Morphological and anatomical changes in plants as a response to salinity stress. − In: Poljakoff-Mayber A., Gale J. (ed.): Plants in Saline Environments. Pp. 97-117. Springer, Berlin – Heidelberg 1975.

Porcel R., Redondo-Gómez S., Mateos-Naranjo E. *et al*.: Arbuscular mycorrhizal symbiosis ameliorates the optimum quantum yield of photosystem II and reduces non-photochemical quenching in rice plants subjected to salt stress. − J. Plant Physiol. **185**: 75-83, 2015.

Pospíšil P.: Production of reactive oxygen species by photosystem II. − BBA-Bioenergetics **1787**: 1151-1160, 2009.

Prins A., van Heerden P.D.R., Olmos E. *et al*.: Cysteine proteinases regulate chloroplast protein content and composition in tobacco leaves: a model for dynamic interactions with ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) vesicular bodies. − J. Exp. Bot. **59**: 1935-1950, 2008.

Purty R.S., Kumar G., Singla-Pareek S.L. *et al*.: Towards salinity tolerance in *Brassica*: an overview. − Physiol. Mol. Biol. Plants **14**: 39-49, 2008.

Qadir M., Quillérou E., Nangia V. *et al*.: Economics of salt-induced land degradation and restoration. − Nat. Resour. Forum **38**: 282-295, 2014.

Rabhi M., Castagna A., Remorini D. *et al*.: Photosynthetic responses to salinity in two obligate halophytes: *Sesuvium*

portulacastrum and *Tecticornia indica*. − S. Afr. J. Bot. **79**: 39-47, 2012.

Rabhi M., Hafsi C., Lakhdar A. *et al*.: Evaluation of the capacity of three halophytes to desalinize their rhizosphere as grown on saline soils under nonleaching conditions. − Afr. J. Eco. **47**: 463-468, 2009.

Rahman H., Jagadeeshselva N., Valarmathi R. *et al*.: Transcriptome analysis of salinity responsiveness in contrasting genotypes of finger millet (*Eleusine coracana* L.) through RNA-sequencing. − Plant Mol. Biol. **85**: 485-503, 2014.

Raines C.A.: The Calvin cycle revisited. − Photosynth. Res. **75**: 1-10, 2003.

Ramani B., Zorn H., Papenbrock J.: Quantification and fatty acid profiles of sulfolipids in two halophytes and a glycophyte grown under different salt concentrations. − Z. Naturforsch. **59**: 835-842, 2004.

Rangani J., Parida A.K., Panda A. *et al*.: Coordinated changes in antioxidative enzymes protect the photosynthetic machinery from salinity induced oxidative dand confer salt tolerance in an extreme halophyte *Salvadora persica* L. − Front. Plant Sci. **7**: 50, 2016.

Reddy A.R., Chaitanya K.V., Vivekanandan M.: Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. − J. Plant Physiol. **161**: 1189-1202, 2004.

Redondo-Gómez S., Mateos-Naranjo E., Cambrolle J. *et al*.: Carry-over of differential salt tolerance in plants grown from dimorphic seeds of *Suaeda splendens*. − Ann. Bot.-London **102**: 103-112, 2008.

Sage R.F.: Photosynthetic efficiency and carbon concentration in terrestrial plants: the C4 and CAM solutions. − J. Exp. Bot. **65**: 3323-3325, 2014.

Samira M., Hichem H., Boughalleb F. *et al*.: Effect of salinity-light interaction on the activity of photosystem II of excised leaves of maize. − Afr. Crop Sci. J. **23**: 343-354, 2015.

Sang T., Shan X., Li B. *et al*.: Comparative proteomic analysis reveals the positive effect of exogenous spermidine on photosynthesis and salinity tolerance in cucumber seedlings. − Plant Cell Rep. **35**: 1769-1782, 2016.

Schieber M., Chandel N.S.: ROS function in redox signaling and oxidative stress. − Curr. Biol. **24**: R453-R462, 2014.

Seepratoomrosh J., Pokethitiyook P., Meetam M. *et al*.: The effect of light stress and other culture conditions on photoinhibition and growth of *Dunaliella tertiolecta*. − Appl. Biochem. Biotech. **178**: 396-407, 2016.

Seki M., Ishida J., Narusaka M. *et al*.: Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. − Plant J. **31**: 279-292, 2002.

Senge M.O., Ryan A.A., Letchford K.A. *et al*.: Chlorophylls, symmetry, chirality, and photosynthesis. − Symmetry **6**: 781-843, 2014.

Sengupta S., Majumder A.L.: Insight into the salt tolerance factors of a wild halophytic rice, *Porteresia coarctata*: a physiological and proteomic approach. − Planta **229**: 911-929, 2009.

Shabala S., Cuin T.A., Prismall L. *et al*.: Expression of animal *CED-9* anti-apoptotic gene in tobacco modifies plasma membrane ion fluxes in response to salinity and oxidative stress. − Planta **227**: 189-197, 2007.

Shabala S., Mackay A.: Ion transport in halophytes. − Adv. Bot. Res. **57**: 151-187, 2011.

Shabala S.: Learning from halophytes: physiological basis and strategies to improve abiotic stress tolerance in crops. − Ann. Bot.-London **112**: 1209-1221, 2013.

Sharan A., Soni P., Nongpiur R.C. *et al*.: Mapping the 'Two component system' network in rice. − Sci. Rep. **7**: 9287, 2017.

Sharma P., Jha A.B., Dubey R.S. *et al*.: Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. − J. Bot. **2012**: 217037, 2012.

Sharma R., Mishra M., Gupta B. *et al*.: *De novo* assembly and characterization of stress transcriptome in a salinity-tolerant variety CS52 of *Brassica juncea*. − PLoS ONE **10**: e0126783, 2015.

Shevela D., Björn L.O., Govindjee.: Evolution of the Z-scheme of photosynthesis: a perspective. − Photosynth. Res. **133**: 5-15, 2017.

Shu S., Guo S.R., Sun J. *et al*.: Effects of salt stress on the structure and function of the photosynthetic apparatus in *Cucumis sativus* and its protection by exogenous putrescine. − Physiol. Plantarum **146**: 285-296, 2012

Singh A.K., Kumar R., Pareek A. *et al.*: Overexpression of rice CBS domain containing protein improves salinity, oxidative, and heavy metal tolerance in transgenic tobacco. − Mol. Biotechnol. **52**: 205-216, 2012.

Singla-Pareek S.L., Yadav S.K., Pareek A. *et al*.: Enhancing salt tolerance in a crop plant by overexpression of glyoxalase II. − Transgenic Res. **17**: 171-180, 2008.

Sobhanian H., Motamed N., Jazii F.R. *et al*.: Salt stress induced differential proteome and metabolome response in the shoots of *Aeluropus lagopoides* (Poaceae), a halophyte C4 plant. − J. Proteome Res. **9**: 2882-2897, 2010.

Soda N., Sharan A., Gupta B.K. *et al*.: Evidence for nuclear interaction of a cytoskeleton protein (*OsIFL*) with metallothionein and its role in salinity stress tolerance. − Sci. Rep. **6**: 34762, 2016.

Soni P., Nutan K.K., Soda N. *et al*.: Towards understanding abiotic stress signaling in plants: convergence of genomic, transcriptomic, proteomic, and metabolomic approaches. − In: Paney G.K (ed.): Elucidation of Abiotic Stress Signaling in Plants. Vol. 2. Pp. 3-40. Springer, New York 2015.

Stanley S.M.: An ecological theory for the sudden origin of multicellular life in the late Precambrian. − P. Natl. Acad. Sci. USA **70**: 1486-1489, 1973.

Stebbins G. L.: Chromosomal variation and evolution. − Science **152**: 1463-1469, 1966.

Stepien P., Johnson G.N.: Contrasting responses of photosynthesis to salt stress in the glycophyte *Arabidopsis* and the halophyte *Thellungiella*: role of the plastid terminal oxidase as an alternative electron sink. − Plant Physiol. **149**: 1154-1165, 2009.

Strogonov B.P.: Physiological Basis of Salt Tolerance of Plants (as Affected by Various Types of Salinity). Pp. 279. Akademia Nauk SSSR, Moskva 1964.

Sudhir P.R., Pogoryelov D., Kovacs L. *et al*.: The effects of salt stress on photosynthetic electron transport and thylakoid membrane proteins in the cyanobacterium *Spirulina platensis*. − J. Biochem. Mol. Biol. **38**: 481-485, 2005.

Suga M., Akita F., Hirata K. *et al*.: Native structure of photosystem II at 1.95 A resolution viewed by femtosecond X-ray pulses. − Nature **517**: 99-103, 2015.

Sultana N., Ikeda T., Itoh R.: Effect of NaCl salinity on photosynthesis and dry matter accumulation in developing rice grains. − Environ. Exp. Bot. **42**: 211-220, 1999.

Takache H., Pruvost J., Marec H.: Investigation of light/dark cycles effects on the photosynthetic growth of *Chlamydomonas reinhardtii* in conditions representative of photobioreactor cultivation. − Algal Res. **8**: 192-204, 2015.

Tezara W., Mitchell V.J., Driscoll S.D. *et al*.: Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. − Nature **401**: 914-917, 1999.

Thagela P., Yadav R.K., Mishra V. *et al*.: Salinity-induced inhibition of growth in the aquatic pteridophyte *Azolla microphyll*s primarily involves inhibition of photosynthetic components and signaling molecules as revealed by proteome analysis. − Protoplasma **254**: 303-313, 2017.

Theerawitaya C., Samphumphaung T., Cha-Um S. *et al*.: Responses of Nipa palm (*Nypa fruticans*) seedlings, a mangrove species, to salt stress in pot culture. − Flora **209**: 597-603, 2014.

Thomas B.J., Gest H., Govindjee.: Celebrating the millennium – historical highlights of photosynthesis research. − Photosynth. Res. **73**: 1-6, 2002.

Tripathi A.K., Pareek A., Singla-Pareek S.L.: A NAP-family histone chaperone functions in abiotic stress response and adaptation. − Plant Physiol. **171**: 2854-2868, 2016.

Udovenko G.V., Mashanskiĭ V.F., Sinitskaya I.A.: Changes of the root cell ultrastructure in plants with different salt tolerance during salinization. − Fiziol. Rast. **17**: 975-981, 1970.

United Nation University Institute for Water, Environment and Health (UNU-INWEH) report. Pp. 26. Hamilton, Canada 2014

Vinyard D.J., Ananyev G.M., Dismukes G.C.: Photosystem II: the reaction centre of oxygenic photosynthesis. − Annu. Rev. Biochem. **82**: 577-606, 2013.

Volkov V.: Salinity tolerance in plants. Quantitative approach to ion transport starting from halophytes and stepping to genetic and protein engineering for manipulating ion fluxes. − Front. Plant Sci. **6**: 873, 2015.

von Caemmerer S., Quick W.P., Furbank R.T.: The development of C4 rice: current progress and future challenges. − Science **336**: 1671-1672, 2012.

von Willert D.J., Kramer D.: [Ultrastructure and crassulacean acid metabolism in *Mesembryanthemum crystallinum* leaves during normal and NaCl-induced ageing.] − Planta **107**: 227-237, 1972. [In German]

Wada S., Ishida H., Izumi M. *et al*.: Autophagy plays a role in chloroplast degradation during senescence in individually darkened leaves. − Plant Physiol. **149**: 885-893, 2009.

Wang L., Liang W., Xing J. *et al*.: Dynamics of chloroplast proteome in salt-stressed mangrove *Kandelia candel* (L.) Druce. − J. Proteome Res. **12**: 5124-5136, 2013.

Wang P., Song C.P.: Guard-cell signalling for hydrogen peroxide and abscisic acid. − New Phytol. **178**:703-718, 2008.

Wang Y., Chu Y., Liu G. *et al*.: Identification of expressed sequence tags in an alkali grass (*Puccinellia tenuif*lora) cDNA library. − J. Plant Physiol. **164**: 78-89, 2007.

Wang Y., Nii N.: Changes in chlorophyll, ribulose bisphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in *Amaranthus* tricolor leaves during salt stress. − J. Hortic. Sci. Biotechnol. **75**: 623-627, 2000.

Williams B.P., Aubry S., Hibberd J.M.: Molecular evolution of genes recruited into C(4) photosynthesis. − Trends Plant Sci. **17**: 213-220, 2012.

Willows R.D., Li Y., Scheer H. *et al*.: Structures of chlorophyll f. − Org. Lett. **15**: 1588-90, 2013.

Wu H., Shabala L., Barry K. *et al*.: Ability of leaf mesophyll to retain potassium correlates with salinity tolerance in wheat and barley. − Physiol. Plantarum **149**: 515-527, 2013.

Yamane K., Taniguchi M., Miyake H.: Salinity-induced subcellular accumulation of H_2O_2 in leaves of rice. − Protoplasma **249**: 301-308, 2012.

Yamori W., Shikanai T.: Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. − Annu. Rev. Plant Biol. **67**: 81-106, 2016.

Yang C., Zhao L., Zhang H. *et al*.: Evolution of physiological responses to salt stress in hexaploid wheat. − P. Natl. Acad. Sci. USA **12**: 11882-11887, 2014.

Yi X., Sun Y., Yang Q. *et al*.: Quantitative proteomics of *Sesuvium portulacastrum* leaves revealed that ion transportation by V-ATPase and sugar accumulation in chloroplast played crucial roles in halophyte salt tolerance. − J Proteomics **99**: 84-100, 2014.

Yoshida T., Mogami J., Yamaguchi-Shinozaki K.: ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. − Curr. Opin. Plant Biol. **21**: 133-139, 2014.

Yu Y., Assmann S.M.: The effect of NaCl on stomatal opening in *Arabidopsis* wild type and agb1 heterotrimeric G-protein mutant plants. − Plant Signal. Behav. **11**: e1085275, 2016.

Zhang Y., Lai J., Sun S. *et al*.: Comparison analysis of transcripts from the halophyte *Thellungiella halophila*. − J. Integr. Plant Biol. **50**: 1327-1335, 2008.

Zhang Y.M., Ma H.L., Calderón-Urrea A. *et al*.: Anatomical changes to protect organelle integrity account for tolerance to alkali and salt stresses in *Melilotus officinalis*. − Plant Soil **406**: 327-340, 2016.