

Physiological adaptive mechanisms of plants grown in saline soil and implications for sustainable saline agriculture in coastal zone

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Abstract There is large area of saline abandoned and low-yielding land distributed in coastal zone in the world. Soil salinity which inhibits plant growth and decreases crop yield is a serious and chronic problem for agricultural production. Improving plant salt tolerance is a feasible way to solve this problem. Plant physiological and biochemical responses under salinity stress become a hot issue at present, because it can provide insights into how plants may be modified to become more tolerant. It is generally known that the negative effects of soil salinity on plants are ascribed to ion toxicity, oxidative stress and osmotic stress, and great progress has been made in the study on molecular and physiological mechanisms of plant salinity tolerance in recent years. However, the present knowledge is not easily applied in the agronomy research under field environment. In this review, we simplified the physiological adaptive mechanisms in plants grown in saline soil and put forward a

practical procedure for discerning physiological status and responses. In our opinion, this procedure consists of two steps. First, negative effects of salt stress are evaluated by the changes in biomass, crop yield and photosynthesis. Second, the underlying reasons are analyzed from osmotic regulation, antioxidant response and ion homeostasis. Photosynthesis is a good indicator of the harmful effects of saline soil on plants because of its close relation with crop yield and high sensitivity to environmental stress. Particularly, chlorophyll a fluorescence transient has been accepted as a reliable, sensitive and convenient tool in photosynthesis research in recent years, and it can facilitate and enrich photosynthetic research under field environment.

Keywords Photosynthesis · Oxidative stress · Osmotic stress · Ion homeostasis · Ecological engineering

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Abbreviations

ABA	Absciscic acid
AsA	Ascorbate
APX	Ascorbate peroxidase
CAT	Catalase
DHAR	Dehydroascorbate reductase
GPXs	Glutathione peroxidases
GR	Glutathione reductase
GSH	Glutathione
H ₂ O ₂	Hydrogen peroxide
MDA	Malondialdehyde
MDAR	Monoascorbate reductase
O ₂ ⁻	Superoxide anion radical
-OH	Hydroxyl radical
PSI	Photosystem I
PSII	Photosystem II
ROS	Reactive oxygen species
SOD	Superoxide dismutase

Introduction

Human beings have stridden into the 21st century, and challenges concomitant with opportunities turn up in front of us. The most important challenges are how to supply enough food for the growing population, how to reduce the environmental pollution along with the rapid growth of industrial production, and how to alleviate the negative effects of global change. In response to these challenges, the concept of sustainable development was brought forward, and so far, great efforts have been made under the support of big projects such as *Arabidopsis* Genome Plan, FACE Project, Rice Genome Project and so on (Ausubel and Benfey 2002; Dixon 2005; Stewart 2005; Van Montagu 2005; Pokorny et al. 2011). These projects made use of biological methods to realize sustainable development. As a result, the development of biological science including molecular biology and plant stress physiology was promoted.

At present, more than 800 million hectares land in the world is affected by salinity (FAO 2008). This amount accounts for more than 6 % of the world's total land area, and the saline land extends over all the continents including Africa, Asia, Australasia, and America. In contrast to animals, plants cannot escape from the negative surroundings and have to acclimatize themselves to the changing environments through a series of physiological process (Dufty et al. 2002; Meyerowitz 2002; Glombitza et al. 2004; Shao et al. 2006; Jaleel et al. 2009). Among the environmental stress, more attention should be paid to soil salinity, as it inhibits plants' growth greatly and immediately and large area such as coastal zone is threatened by soil salinity. In recent years, plants possessing high economic value and salt tolerance have been recommended as ecoengineering tools for alternative agricultural production and re-vegetation in salt-affected coastal zone or saline farmland (He et al. 2003; Almodares et al. 2008; Long et al. 2008, 2009; Ruan et al. 2008; Li et al. 2010; Wu et al. 2012). It is crucial to investigate their physiological responses and adaptive mechanisms under saline environment for making proper planting protocol.

Plant salt tolerance mechanism was firstly reviewed by Flowers et al. (1977). From then on, many reviews have been published along with the gradual research advancement on this issue (Greenway and Munns 1980; Hasegawa et al. 2000; Zhu 2003; Chaves et al. 2009; Chen and Polle 2010). Recently, Munns and Tester (2008) reviewed the mechanisms of plant salt tolerance at the molecular, cellular, and whole plant levels in detail, and proposed that it was a great opportunity for plant salt tolerance researchers to link new molecular techniques together with whole plant physiology. Turkan and Demiral (2009) also presented a brief depiction about molecular mechanisms of salt stress signaling from the perception and signaling pathways for

ion homeostasis to the respective responses at the antioxidant level and compensatory mechanisms for osmotic homeostasis. However, the plant physiological mechanisms in these reviews seem exclusive and elusive, and they are not easily applied in the field study. In this review, we simplified the mechanisms and put forward a practical procedure for discerning physiological status and adaptive physiological responses in plants grown in saline soil, and it can benefit saline agricultural development and ecological engineering planning. In our opinion, the process of salt stress on plant can be summarized into three aspects. First, saline soil leads to the decrease in water status of soil solution, which makes plants hard to take up water from the soil. Second, salt stress may induce the increase of Na^+ and Cl^- concentration in the cytosol, and these toxic ions can negatively affect enzymes and lipids in the cells. When Na^+ and Cl^- concentrations increase to the toxic threshold, cells tend to die. At last, high soil salt concentration can induce leaf stomatal closure, and photoinhibition may occur due to the feedback of inhibited CO_2 fixation, which can bring about the oxidative stress in the chloroplast. Oxidative stress also can occur in the roots probably due to the elevated respiration rate. To our knowledge, physiological mechanisms of salt tolerance are to minimize the accumulation of toxic ions in plant tissue, partition them in the apoplast and vacuole for avoiding toxic concentrations in the cytosol of transpiring leaves, increase the synthesis of osmotic metabolites such as proline and betaine for maintaining tissue water status, and enhance antioxidant capacity to prevent the occurrence of oxidative stress. However, it is still not clear about the parameters which can appropriately represent the harmful effects of salt stress on plants and also be conveniently measured. We propose that plant biomass, crop yield and photosynthesis are the most reasonable candidates, because plant growth and food production mainly depend on them. It should be stressed that photosynthetic diagnosis becomes a very convenient way to detect the plant health status, particularly after the exploitation of chlorophyll a fluorescence transient. In addition, the adaptive mechanisms in responses to salinity-induced negative effects were generalized and simplified, and some representational parameters were suggested in this review.

Plant biomass and photosynthesis

Decrease of plant biomass was commonly induced by environmental stress including salinity stress (D'Souza and Devaraj 2010; Gorai et al. 2011; Tarchoune et al. 2012). It is a traditional and comprehensive index for the negative effects on plant in adverse environment. However, plant biomass is not a sensitive parameter, because the decrease

in biomass accumulation results from long-term effect of adverse environment. Photosynthesis is closely related to plant growth and crop yields and highly sensitive to environmental stress as well. Photosynthesis involves the parts of CO₂ fixation, photosynthetic electron transport for reducing power, and proton transport for adenosine triphosphate generation. Photosynthetic rate would decrease if any part of photosynthesis was inhibited under environmental stress. Decrease in photosynthetic activity can be commonly found in plants under salt stress, which is often induced by various reasons. Initial negative effect of salt stress on photosynthesis may be the decreased CO₂ availability as a result of the diffusion limitations of stomata (Flexas et al. 2004; Dasgupta et al. 2011; Benzarti et al. 2012; Tarchoune et al. 2012). Stomatal conductance responds to soil salinity owing to the perturbed water relations or the synthesis of abscisic acid (ABA) (Fricke et al. 2004). It has been reported that ABA increased in the photosynthetic tissues transiently within 10 min of the addition of 100 mM NaCl to barley (Fricke et al. 2004, 2006). The rapid increase suggested that ABA was synthesized in situ rather than transported from the roots. In addition, salt stress also can reduce the mesophyll conductance to CO₂, and then result in the decrease of photosynthetic rate (Loreto et al. 2003). The resistance of the chloroplast envelope and stroma is mainly responsible for the total mesophyll resistance, and it is also influenced by respiratory and photorespiratory CO₂ diffusing toward the chloroplasts from the mitochondria (Tholen et al. 2012). The dark enzymatic process of CO₂ fixation can be directly perturbed by salt stress, for example, the decrease in Rubisco activity and content (Downton et al. 1985; Brugnoli and Bjorkman 1992; Yang et al. 2008; Tarchoune et al. 2012). Photosystem II (PSII) plays an important role in plant photosynthesis, and it often operates abnormally under environmental stress. So far, great efforts have been made to figure out PSII responses to salt stress, however, inconsistent results were obtained. PSII function was proved to be inhibited by salt stress in some studies (Belkhdja et al. 1994; Everard et al. 1994; Netondo et al. 2004; Benzarti et al. 2012), whereas high resistance of PSII to salt stress was demonstrated in other studies (Morales et al. 1992; Lu et al. 2002, 2003a, b; Chen et al. 2004; Tarchoune et al. 2012). Different plant species used in these studies may be one of the reasons leading to the inconsistent results. Up to now, the responses of photosystem I (PSI) have not been well elucidated under salt stress. PSI performance, particularly the interaction between PSI and PSII under salt stress in plants may become a new interesting research issue in the future.

Gas exchange and chlorophyll a fluorescence are the main tools for plant photosynthetic analysis, particularly under environmental stress. A series of commercial

portable open gas exchange systems with options for controlling CO₂, humidity, temperature, and light have entered the markets (e.g., LI-6400, Li-Cor Inc., Lincoln, Nebraska, USA; CIRAS-II, PP, System, Hitchin, UK). These off-the-shelf portable systems provide real-time measurements of CO₂ uptake, transpiration, leaf conductance, and the intercellular CO₂ mol fraction. Modulated fluorometer (Hansatech, UK; Palm, Waze) and non-modulated fluorometer (Handy PEA, PEA Senior, M-PEA) also have been widely used for analyzing the properties of photosynthetic apparatus, and these instruments greatly promote the photosynthetic research. Under salt stress, gas exchange and chlorophyll a fluorescence are widely adopted to detect the negative effects on plant photosynthesis. Chlorophyll a fluorescence transient (O–J–I–P) is the kinetics of fast fluorescence rise process and can be measured by Handy PEA or PEA (Fig. 1). O–J–I–P transient has been accepted as a reliable and popular tool in photosynthetic research, especially to study PSII behavior in recent years (Wen et al. 2005; Strauss et al. 2007; Toth et al. 2007; Yang et al. 2007; Chen et al. 2008; Rapacz et al. 2008; Yan et al. 2008, 2011; Li et al. 2009; Mehta et al. 2010; Rapacz et al. 2010; Jedmowski et al. 2013). O, J, I and P are a sequence of phases in the kinetics of fast fluorescence rise, and environmental stress often provokes the occurrence of K phase in this transient, suggesting the damage to oxygen-evolving complex in donor side of PSII (Strasser et al. 2004). A method called JIP test has been developed for quantification of OJIP transient using fluorescence intensity in these phases (Strasser et al. 2004). This test is a powerful tool for in vivo investigation of the whole PSII function including fluxes of absorption, trapping, and electron transport. In addition, it can show heterogeneous behaviors of PSII components including reaction centers, donor side and acceptor side under environmental stress. More recently, PEA Senior and M-PEA have been designed, and they can tell us not only the information from JIP test but also the changes in PSI, since chlorophyll a fluorescence and 820 nm transmission kinetics can be simultaneously recorded (Fig. 2). This technology will extend our knowledge about PSI and the cooperation between PSI and PSII and give us a more thorough and comprehensive picture about the operating mechanisms of plant photosynthetic apparatus (Zhang et al. 2011; Yan et al. 2012). It is noticeable that CO₂ fixation process is also a critical step for photosynthesis (Salvucci and Crafts-Brandner 2004). Rubisco enzyme and its activation enzyme play a key role in this step, and their activities and contents can be measured, but the procedure is relatively complex. However, carboxylation efficiency can be measured using portable open gas exchange systems, and this parameter can indirectly reflect the performance of Rubisco enzyme (Voncaemmerer and Farquhar 1981).

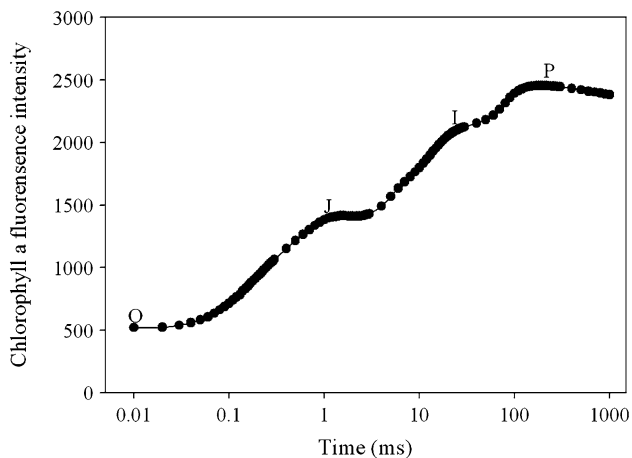


Fig. 1 Chlorophyll a fluorescence transient measured by Handy PEA in a newly expanded leaf of sorghum. O, J, I and P indicate the specific steps in this transient

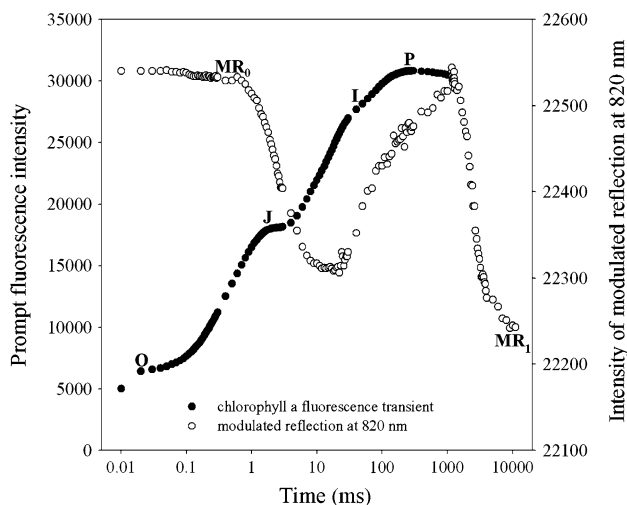


Fig. 2 Kinetics of prompt fluorescence and modulated 820 nm reflection detected by M-PEA in a fully expanded leaf of Jerusalem artichoke. MR_0 is the value of modulated 820 nm reflection at the onset of red light illumination (0.7 ms, the first reliable MR measurement). MR_1 is the value of modulated 820 nm reflection after far-red light illumination. O, J, I and P indicate the specific steps in chlorophyll a fluorescence transient

In conclusion, photosynthesis and biomass should be taken as the criterion for judging negative effects of salinity on plants. How salinity exerts harmful effects on plants and the corresponding physiological regulation ways is elucidated in the following paragraphs.

Osmotic regulation under salt stress

Osmotic stress on plants dose not only occur in drought land such as physiological drought which is hard to absorb water, can also be induced by salinity. Large quantity of

ions in the saline land reduces its water status, so it is difficult for roots to collect water. As a consequence, most important metabolism including photosynthesis and cell division in plants would be affected or inhibited. Active responses are necessary for plants to survive under this adverse condition.

Lots of metabolites are accumulated in plants, which are considered as “compatible (organic) solutes” in the cytoplasm to increase their hyperosmotic tolerance for avoiding water loss from the cells induced by salinity. Various compounds have been suggested to accomplish this function in plants, and they include sugars, sugar alcohols, complex sugars, quaternary amino acid derivatives, tertiary amines and sulfonium compounds (Flowers and Colmer 2008). The compatible solutes are mainly distributed in cytosol to balance the high concentration of salt outside the cell and compensate the high concentrations of salt ions in the vacuole. In contrast to many halophyte plants, the capacity to accumulate compatible solutes in glycophyte plants is not enough, and as a result, they are more susceptible to salt stress.

Proline and glycinebetaine belong to tertiary amines. Ashraf and Foolad (2007) have illustrated their synthesis process in detail and summarized their important protective function under abiotic stress. The major role of proline and glycinebetaine is accepted as the metabolites in plants grown in saline soil (Venkatesan and Chellappan 1998; Mansour 2000; Mohanty et al. 2002; Yang et al. 2003; Yang and Lu 2005; Koskeroglu and Tuna 2010; Chakraborty et al. 2012). Glycinebetaine is synthesized in chloroplast and it possesses protective function for thylakoid membrane and photosynthetic apparatus. Increase in glycinebetaine concentration was commonly observed under salt stress in many crop plants, such as sugar beet (*Beta vulgaris*), spinach (*Spinacia oleracea*), barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), and sorghum (*Sorghum bicolor*) (Weimberg et al. 1984; Fallon and Phillips 1989; Yang et al. 2003). Exogenous application of glycinebetaine can help reduce adverse effects in maize subjected to salt stress (Yang and Lu 2005). Similarly, increase in proline content was observed in plants under salinity condition, and it is involved in alleviating cytoplasmic acidosis and sustaining $NADP^+/NADPH$ ratios at required levels for metabolism and thus supporting redox cycling (Babiychuk et al. 1995; Hare and Cress 1997). Salt stress remarkably increased proline accumulation in leaves of two rice cultivars with different salinity tolerance, and the increase rate was higher in the tolerant one (Demiral and Turkan 2004). Our recent study also illustrated that proline concentration was accumulated to a higher level in sorghum leaves subjected to salt stress, and the increased proline helps counteract the negative effects of high temperature stress on sorghum (Yan et al. 2012). Similarly, this

cross tolerance was also demonstrated in the study on salinity tolerance in dogwood (Renault 2012). In conclusion, proline and glycinebetaine are appropriate indicators for osmotic regulation in plants grown in saline soil.

To maintain normal water content, plants accumulate high concentrations of compatible solutes to regulate water status in cells in response to the salt-induced osmotic stress. Water potential, glycinebetaine and proline contents in leaf and root are important candidates for detecting osmotic regulation under salinity stress. Water potential can be detected using dew point water potential instrument, while glycinebetaine and proline contents can be determined using spectrophotometer and high-performance liquid chromatography.

Oxidative stress induced by salt stress

Similar to other environmental stress, salt stress can also induce the increase of reactive oxygen species (ROS) and then lead to oxidative damage in plant cells. ROS are partially reduced forms of atmospheric oxygen. They typically result from the excitation of O_2 to form singlet oxygen or from the transfer of one, two or three electrons to O_2 to form a superoxide radical (O_2^-), hydrogen peroxide (H_2O_2) or a hydroxyl radical ($-OH$), respectively. In contrast to atmospheric oxygen, ROS are capable of unrestricted oxidation of various cellular components and can lead to the oxidative destruction in plant cells (Mittler 2002). ROS are generated in the normal metabolism in plant cells, and there are many potential sources of ROS. Photosynthetic electron transport and respiration process are the major origins of ROS production in plant cells. Under normal growth conditions, ROS production is low, but it may increase under environmental stress. Plants have evolved a suite of protective systems—antioxidant system—to keep ROS under control under normal growth conditions. Consequently, the antioxidant system is considered to play a fundamental role in mediating environmental stress resistance (Tausz et al. 2007; Jaleel et al. 2009). Antioxidant system consists of small molecular antioxidants and antioxidant enzymes. Superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (APX, EC 1.11.1.11), glutathione peroxidases (GPXs, EC 1.11.1.9) and catalase (CAT, EC 1.11.1.6) are crucial ROS-scavenging enzymes in plant cells. SOD catalyzes the dismutation of O_2^- to molecular oxygen and H_2O_2 , which can be subsequently scavenged by APX and CAT. They work together to control the concentrations of O_2^- and H_2O_2 , which then limit the generation of $-OH$, the most dangerous species of all the ROS (Mittler 2002). As the major antioxidants, ascorbate (AsA) and glutathione (GSH) can directly scavenge ROS and act as reducing substrate for

APX and GPXs to detoxify H_2O_2 . Glutathione reductase (GR), dehydroascorbate reductase (DHAR) and monoascorbate reductase (MDAR) act as antioxidant-regenerating enzymes, and they cooperate to regenerate GSH and AsA from their oxidized forms at the expense of reducing power (Mittler 2002).

If ROS production induced by environmental stress overwhelmed the scavenging capability of antioxidant system, oxidative damage would occur. Oxidative stress often occurred in plants under salinity condition. Under salinity stress, availability of atmospheric CO_2 declined because of the increased stomatal closure, and subsequently, NADPH consumption by the Calvin cycle decreased. When ferredoxin is over-reduced during photosynthetic electron transfer, electrons may be transferred to oxygen to form O_2^- by the process called Mehler reaction, and subsequently, more harmful oxygen radicals may be generated through chain reactions (Hsu and Kao 2003; Shao et al. 2008). Under oxidative stress, plants can detoxify the excess ROS by accumulating the contents of antioxidants such as AsA and GSH and by up-regulating the activities of antioxidant enzymes such as SOD, APX and CAT. Consequently, a degree of cellular oxidative damage in plants resulting from abiotic stress is mediated (Turkan et al. 2005). It has been reported that salinity tolerance is closely related to antioxidant capacity in many plant species (Gossett et al. 1994; Hernandez et al. 1995; GuetaDahan et al. 1997; Dionisio-Sese and Tobita 1998; Meneguzzo et al. 1999; Hernandez et al. 2000; Sreenivasulu et al. 2000; Shalata et al. 2001; Bor et al. 2003; Mittova et al. 2003; Demiral and Turkan 2004, 2005; Koca et al. 2006, 2007; Sekmen et al. 2007; Yazici et al. 2007; Chen et al. 2010). In addition, transgenic plants over-expressing ROS-scavenging enzymes such as SOD (Badawi et al. 2004; Tseng et al. 2007), CAT (Tseng et al. 2007), APX (Wang et al. 1999) and GR (Foyer et al. 1995) showed enhanced tolerance to the oxidative stresses in plants under adverse conditions.

It should be noticed that phenolics also can work as antioxidant because of their free-radical trapping properties (Treutter 2006). The importance of phenolics accumulation in resisting salt-induced oxidative stress has been demonstrated (Wahid and Ghazanfar 2006; Ksouri et al. 2007). Recently, Abrol et al. (2012) reported that secondary metabolite contents were initially increased compared with the later increase in antioxidant enzymes activities, when *Swertia chirata* Buch.-Ham. was subjected to salinity stress. Biochemical relationship between the induction of antioxidant enzymes and production of secondary metabolites in plants exposed to salinity can be further discussed in the future.

Lipid peroxidation level which was determined in terms of malondialdehyde content is a classic parameter to

indicate the oxidative damage to membrane lipids in cells. Contents of H_2O_2 and O_2^- can also be easily measured by biochemical methods. Ordinary antioxidant enzymes, SOD, CAT, GPXs and APX, as well as AsA and GSH contents can be conveniently assayed using spectrophotometer and high-performance liquid chromatography. Phenolics are composed of many types of components such as flavonoid, lutein, tannin and so on, and their contents also can be detected using high-performance liquid chromatography.

K^+ and Na^+ homeostasis under salt stress

The homeostasis of intracellular ion concentrations is critical for the metabolism of living cells. Plant cells have to keep the concentrations of toxic ions low and accumulate essential ions through proper regulation of ion flux. Na^+ is toxic to the plant cells because of the similarity in physicochemical properties between Na^+ and K^+ . Na^+ competes with K^+ for major binding sites in key metabolic processes in the cytoplasm, such as enzymatic reactions, protein synthesis and ribosome functions (Munns and Tester 2008).

Active transport mediated by H^+ -ATPase and secondary transport with channels and co-transporters have been evolved in plant cells to maintain high K^+ concentration and low Na^+ concentrations in the cytosol. Na^+ exclusion from cells and compartmentation of excessive Na^+ in vacuole are important protective ways in response to ion toxicity induced by salt stress at the cellular level. As a whole body to adapt to salt stress, plants can preserve Na^+ in the roots and restrict Na^+ flux to the shoot or leaves, and in addition, more Na^+ may be loaded into the organs or tissues with less physiological activity such as senescing leaves, leaf sheath or epidermis. In some halophytes, leaves or stems can evolve to be succulent for diluting the concentration of toxic ions, and salt glands or bladders may be distributed in the shoot for the secretion of excess ions. Recently, the molecular regulation and physiological mechanisms to maintain normal K^+ and Na^+ homeostasis in plant cells have been reviewed in detail (Tester and Davenport 2003; Zhu 2003; Apse and Blumwald 2007; Shabala and Cuin 2008), and it is not required to repeat again. However, there is no confessed way to indicate the capability to coordinate K^+ and Na^+ homeostasis in plant cells.

Under salt stress, increase in Na^+ concentration and decrease in K^+ concentration are often observed in plant leaves. Islam et al. (2007) and Luo et al. (2005), respectively, demonstrated that salt-tolerant wheat and wild soybean can maintain lower level of Na^+ concentration in leaves by withholding Na^+ in the roots and stems. Thus,

the level of Na^+ and K^+ in leaves can be accepted as an indicator to evaluate the capability to resist ion toxicity in plant under salt stress. However, Shabala and Cuin (2008) did not fully agree with the above viewpoint, and they believed that it was not the absolute quantity of Na^+ but rather the cytosolic K^+/Na^+ ratio determining cell metabolic competence and the ability of a plant to survive in saline environments. Indeed, the cytosolic K^+/Na^+ ratio has been repeatedly referred as an important indicator for plant salt tolerance (Gorham et al. 1991; Gaxiola et al. 1992; Dvorak et al. 1994; Maathuis and Amtmann 1999; Cuin et al. 2003; Colmer et al. 2006); however, less direct experimental evidence can be found to support it due to no proper measuring protocol. The major hurdle is the lack of appropriate and convenient techniques to enable such compartmentation analysis for differentiating K^+ and Na^+ in vacuole from those in the cytoplasm. So far, although non-invasive micro-test technique, energy-dispersive X-ray microanalysis and multi-barreled microelectrodes have been employed (Shabala et al. 2006), it is hard to carry out these methods in ordinary labs due to the expensive instruments.

Conclusions and prospects

The harmful effects of salt stress on plants are related to osmotic stress, Na^+ toxicity, nutritional imbalance and oxidative stress. Fortunately, plants can ameliorate these adverse effects by physiological regulation. Plants accumulate compatible organic solutes such as glycinebetaine and proline to reduce cell water potential in response to osmotic stress. Antioxidant system can be activated to protect themselves against the attack from ROS under salt stress. In addition, active transport and secondary transport with channels and co-transporters have been evolved in plant cells to maintain characteristically high concentration of K^+ and low concentrations of Na^+ in the cytosol. Thus, the procedure for investigating physiological status in plants grown in saline soil can be concluded in two steps. First, negative effects are evaluated by the salt stress on biomass, crop yield and photosynthesis. Second, the underlying reasons are analyzed from three aspects including osmotic regulation, antioxidant response and ion homeostasis.

To make out the genetic and physiological responses in plants under salt tolerance is only the first step in developing a more salt-tolerant crop. Enhancing plant salt tolerance is a crucial step for culturing crops in saline land, and there are three methods—conventional breeding program, gene engineering method and ordinary physiological methods. Due to the complexity of functional genes in response to salt stress, conventional breeding program is

Table 1 Eco-physiological means for improving plant salinity tolerance

Eco-physiological means	Plant materials	References
Addition of K ⁺ and Ca ²⁺	Sunflower, <i>Rumex</i> , tomato, melon, wheat	Chen et al. (2007), Kaya et al. (2007), Zheng et al. (2008), Akram and Ashraf (2011), Fan et al. (2011)
NaCl pretreatment	Sorghum; soybean	Amzallag et al. (1990), Umezawa et al. (2000)
Application of ascorbic acid	Wheat	Athar et al. (2008)
Pretreatment with H ₂ O ₂ , ethylene, hemin, paraquat and glutamate	Cucumber, wheat	Wahid et al. (2007), Chang et al. (2010), Lin et al. (2011), Xu et al. (2011)
Application of polyamine	Rice	Chattopadhyay et al. (2002)
Application of phosphorus and humic acid	Pepper	Cimrin et al. (2010)
Application of glycinebetaine or proline	Maize, rice, melon, canola	Sakr et al. (2012), Yang and Lu (2005), Demiral and Turkan (2006), Kaya et al. (2007)
Application of salicylic acid	Mungbean, periwinkle	Khan et al. (2010), Nazar et al. (2011), Idrees et al. (2011)
Application of silicon	Rose	Reezi et al. (2009)

H₂O₂, hydrogen peroxide

relatively hard to be executed effectively (Flowers 2004; Shabala and Cuin 2008; Shao et al. 2009, 2010). Although many studies have announced that salt tolerance was enhanced in transgenic plants (Begcy et al. 2011; Hao et al. 2011; Jacobs et al. 2011; Rahnama et al. 2011; Wei et al. 2011), the results are obtained under abnormal growth condition and not tested in the field. Stress resistance training and exogenous application of growth and osmotic regulators have been demonstrated to ameliorate plant salt stress (Amzallag et al. 1990; Umezawa et al. 2000; Chattopadhyay et al. 2002; Demiral and Turkan 2006; Chen et al. 2007; Kaya et al. 2007; Wahid et al. 2007; Athar et al. 2008; Zheng et al. 2008; Reezi et al. 2009; Chang et al. 2010; Cimrin et al. 2010; Khan et al. 2010; Akram and Ashraf 2011; Fan et al. 2011; Idrees et al. 2011; Lin et al. 2011; Nazar et al. 2011; Sakr et al. 2012). These methods are derived from plant eco-physiology theories and are generalized in Table 1. In the future, more attention should be paid to eco-physiological ways for enhancing plant salt tolerance, because they are easy for applying in agronomy practice and ecological restoration in addition to the low cost.

Author contribution This review paper was accomplished with the collaboration of all authors. Kun Yan and Prof. Hongbo Shao defined the research topic on the basis of our previous work, and made tables and figures and wrote the primary paper. Chuyang Shao searched the literature and provided improved version by correcting the revised manuscript. Peng Chen participated in discussions and wrote about two paragraphs of the review and Xiaobing Chen provided comments on the first manuscript. Prof. Hongbo Shao and Prof. Shijie Zhao critically reviewed the paper and proposed some useful suggestions. Prof. Marian Brestic carefully polished the language and

proofread this paper. All authors have read and approved the final manuscript.

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