

Plant Responses in Saline and Arid Environments: An Overview

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ABSTRACT

Salinity is the most serious threat to agriculture and to the environment in many parts of the world. It is estimated that over 6% of the world's land is affected by either salinity or sodicity. Using saline lands for conventional agriculture requires either improving the soil or enhancing the salt tolerance limit of field crops, the majority of which cannot survive with the levels of average soil salinity prevailing in the fields. Plants exposed to salt stress undergo changes in their environment. The ability of plants to tolerate salt is determined by multiple biochemical pathways that facilitate retention and/or acquisition of water, protect chloroplast functions, and maintain ion homeostasis. Essential pathways include the synthesis of osmotically active metabolites, specific proteins and certain free radical scavenging enzymes that control ions and water flux and support scavenging of oxygen radicals or chaperones. The ability of plants to detoxify radicals under conditions of salt stress is probably the most critical requirement. Many salt-tolerant species accumulate metabolites which play crucial dual roles as osmoprotectants and as radical scavengers. In this paper, plant responses to salinity stress are reviewed with emphasis on physiological and biochemical mechanisms of salt tolerance. Understanding the biochemical and physiological plant responses to salinity may favour the identification of new salt-tolerant cultivars or species and it provides a framework to identify breeding targets for improving salt tolerance. This review may help in interdisciplinary studies to assess the ecological significance of salt stress.

Keywords: plant growth, rhizosphere, root feature, salinity, stress

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INTRODUCTION

Salinity is abundant in semiarid and arid regions as result of high evaporation of saline underground water or poor irrigation water quality or/and bad irrigation techniques depending on soil properties. The term *salt-affected* refers to soils that are saline or sodic and, according to the FAO Land and Plant Nutrition Management Service, these cover over 400 million ha, which is over 6% of the world land area (**Table 1**). A significant proportion of cultivated land is salt-affected, in fact of the current 230 million ha of irrigated land, 45 million ha are salt-affected (19.5%) and of the 1,500 million ha under dryland agriculture, 32 million are salt-affected to varying degrees (2.1%).

Salinity occurs through natural or human-induced processes that result in the accumulation of dissolved salts in

the soil layers and water to an extent that inhibits plant growth and crop production. The USDA Salinity Laboratory defines a saline soil as having an EC_e of 4.0 dS/m or more which is equivalent to about 40 mM of NaCl in soil saturation extract. There are three major types of salinity based on soil and ground water processes: groundwater associated salinity, transient and irrigation salinity (Rengasamy 2010). Groundwater associated salinity is commonly known as dryland salinity, because it occurs in areas where water, going from depth to the surface of soil, brings dissolved salts. Transient salinity is proper to landscapes where the water-table is deep and the drainage is poor. In this case the concentration of salts in soil layers changes in response to seasonal rainfall, surface evaporation and water use by vegetation. Irrigation salinity is caused by the salts introduced by irrigation water which can accumulate in the root

Table 1 Regional distribution of salt-affected soils, in million hectares.

Regions	Total area		Saline soils		Sodic soils	
	Mha	Mha	%	Mha	%	
	Africa	1,899	39	2.0	34	1.8
Asia, the Pacific and Australia	3,107	195	6.3	249	8.0	
Europe	2,011	7	0.3	73	3.6	
Latin America	2,039	61	3.0	51	2.5	
Near East	1,802	92	5.1	14	0.8	
North America	1,924	5	0.2	15	0.8	
Total	12,781	397	3.1%	434	3.4%	

Source: FAO Land and Plant Nutrition Management Service (1994)

zone. Sodicity is a secondary result of salinity. As sodium is adsorbed by soil particles, above a certain level the soil becomes "sodic" and its structure and hydraulic properties deteriorate.

Salinity effects and problems with regard to tolerance and ecological performance are discussed briefly in this review. Efforts have been made to compare the relative sensitivity of various plant species to salt, and the NaCl uptake and transport are considered with regard to phytotoxicity and interactions with seeds and root apparatus.

FUNCTIONAL ACCLIMATION TO SALT STRESS IN PLANTS

Plants have the ability to take up any salt present in rhizosphere. Na^+ and Cl^- are the ions dominating saline environments, as they predominate in seawaters; sodium, in small quantities, is an essential mineral nutrient only for C4 and CAM plants (Brownell and Crossland 1972). However, with the recent trend of irrigation many crops using recycled water, containing dominant ions other Na^+ , some toxicity or ion imbalance effect are possible (Kennedy and de Filippis 1999; Cayuela *et al.* 2001). High sodium in plants not only retards growth directly but also through interlinked metabolic processes starting from simple enzymatic reactions to more complex molecule building. In such situations, mineral nutrition is disturbed, chlorophyll (Chl) content and their activity reduced, affecting photosynthesis and a host of undesirable events start creeping up and create disturbance in growth and development of plant. All plants show some commonality of traits for salt tolerance: the ability to acquire ions that are then compartmentalized in vacuoles for osmotic adjustment; the ability to regulate the internal Na^+ concentrations through the control of influx and efflux and also discriminating in favor of K^+ over Na^+ (Flowers *et al.* 2010). Halophytes have a tight regulation of ion transport and accumulation. In fact, to adjust the osmotic potential they required Na^+ and Cl^- at toxic concentrations, then the necessity to compartmentalize these ions into vacuoles and to avoid the translocation from roots to shoots. In Fig. 1 are reported the three aspects of salt tolerance in plants (homeostasis, detoxification and growth control) and the pathways that interconnect them; homeostasis is broken down into ionic and osmotic homeostasis. The SOS (Salt-Overly-Sensitive) pathway mediates ion homeostasis and Na^+ tolerance. Perturbations in $[\text{Ca}^{2+}]$ cytosolic level, after perception of salt stress, induce signals that are sensed by SOS3 which interacts with SOS2, a protein kinase. The SOS3/SOS2 complex phosphorylates a plasma membrane Na^+/H^+ antiporter SOS1, which maintains cellular homeostasis by exclusion of the excess Na^+ ions out of cell. A mitogen activated-protein kinase (MAPK) cascade, similar to the yeast HOG1 pathways, is proposed to mediate osmotic homeostasis. The two primary stresses, ionic and osmotic, cause damage or secondary stresses such as oxidation. Lea-type stress proteins such as RD29A are involved in the detoxification mechanisms or damage alleviation. CBF/DREB transcription factors mediate some of the stress protein gene expression in response to secondary stresses caused by high salt concentrations, cold, drought or abscisic

acid (ABA).

Cellular homeostasis is achieved by the coordinated action of many biochemical pathways. However, under sub-optimal conditions stress different pathways can be affected, and their coupling, which makes cellular homeostasis possible, is disrupted (Rizhsky *et al.* 2002). This process is usually accompanied by the formation of reactive oxygen species (ROS) resulting from an increased flow of electrons from the disrupted pathways to the reduction of oxygen (Asada 1999; Dat *et al.* 2000; Mittler 2002). ROS formation leads to changes in intracellular redox homeostasis (Bowler and Fluhr 2000), and it is now widely accepted that redox signals are key regulators of plant metabolism, morphology and development (Foyer and Noctor 2003).

The ROS hydrogen peroxide (H_2O_2) has generally been viewed as a toxic cellular metabolite. However, it is now clear that it may also function as a signal molecule in both plant and animal cells (Finkel 2000; Neill *et al.* 2002). The generation of H_2O_2 is increased in response to a wide variety of abiotic and biotic stresses, and some authors have suggested that H_2O_2 plays a dual role in plants: at low concentrations, it acts as a messenger molecule involved in acclimatory signaling, triggering tolerance against various abiotic stresses, and at high concentrations it orchestrates programmed cell death (Prasad *et al.* 1994; Van Breusegem *et al.* 2001; Vandenabeele *et al.* 2003). Azavedo Neto *et al.* (2005) studied the effect of exogenously applied H_2O_2 on salt stress acclimation with regard to plant growth, lipid peroxidation, and activity of antioxidative enzymes in leaves and roots of a salt-sensitive maize genotype. Pre-treatment by addition of 1 μM H_2O_2 to the hydroponic solution for 2 days induced an increase in salt tolerance during subsequent exposure to salt stress. This was evidenced by plant growth, lipid peroxidation and antioxidative enzymes measurements. In both leaves and roots the variations in lipid peroxidation and antioxidative enzymes (superoxide dismutase, SOD; ascorbate peroxidase, APX; guaiacol peroxidase, POX; glutathione reductase, GR, and catalase, CAT) activities of both acclimated and unacclimated plants, suggested that differences in the antioxidative enzyme activities may, at least in part, explain the increased tolerance of acclimated plants to salt stress, and that H_2O_2 metabolism is involved as signal in the processes of maize salt acclimation. In addition, Szepesi *et al.* (2009) showed that pre-treatment with 10^{-4} M salicylic acid (SA) in hydroponic culture medium provided protection against salinity stress in tomato plants (*Solanum lycopersicum* L. cv. 'Rio Fuego'). The application of 10^{-4} M, SA led to prolonged ABA accumulation and also to higher levels of free putrescine or spermine both in root and leaf tissues, suggesting that polyamines may be implicated in the protection response of the cells, evidencing also an indirect implication of SA. Thus, plant responds to stresses as individual cells and synergistically as a whole organism. Stress induced changes in gene expression in turn may participate in the generation of hormones like ABA, SA and ethylene. These molecules may amplify the initial signal and initiate a second round of signalling that may follow the same pathway or use altogether different components of signaling pathway. Certain molecules also known as accessory molecules may not directly participate in signaling but participate in the modification or assembly of signaling components. These proteins include the protein modifiers, which may be added cotranslationally to the signaling proteins like enzymes for myristoylation, glycosylation, methylation and ubiquitination. Salt response is a multigenic trait thus, the ionic homeostasis, osmotic homeostasis and detoxification pathways are proposed to feed actively into cell division and expansion regulation. Molecules like glycerol and sucrose were discovered by empirical methods to protect biological macromolecules against the damaging effects of salinity. Later, a systematic examination of the molecules, which accumulate in halophytes and halo-tolerant organisms, led to the identification of a variety of molecules also able to provide protection (Sairam and Tyagi 2004). Tobacco plants have been modified by

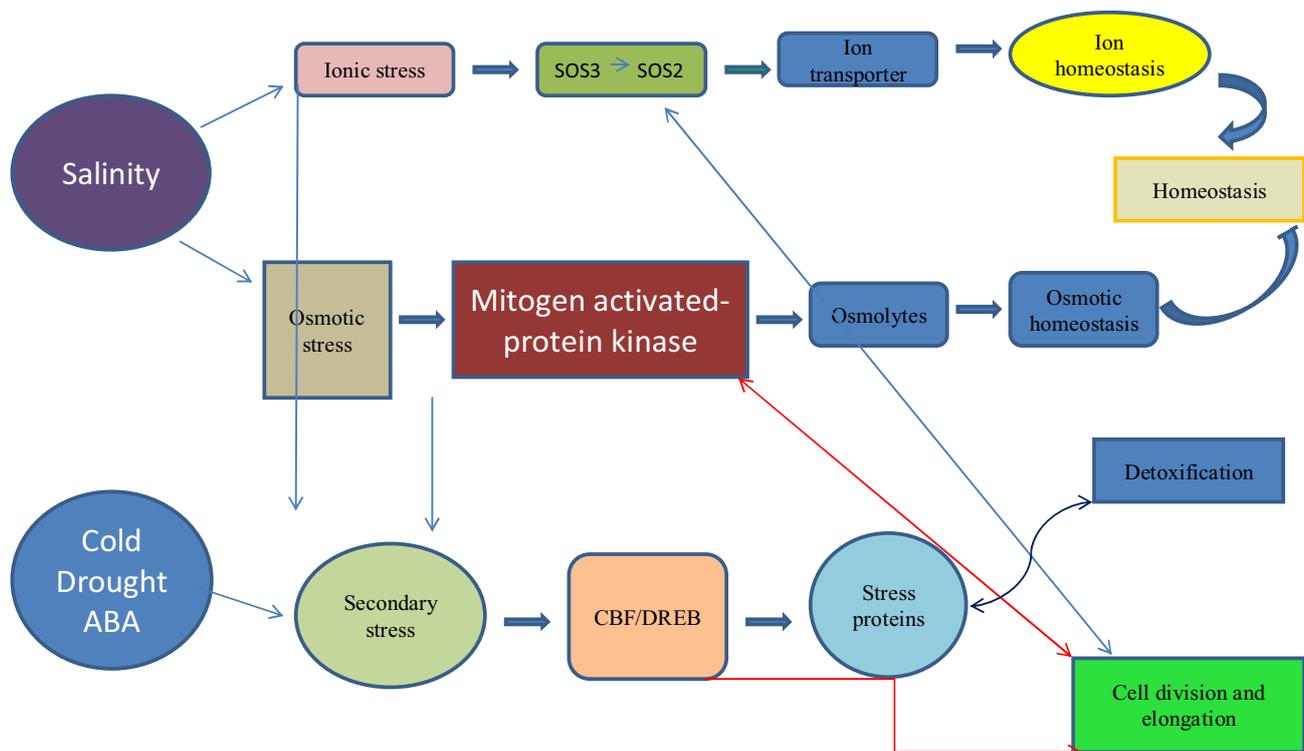


Fig. 1 Homeostasis, detoxification, growth control mechanisms and the pathways that interconnect them in plant under salinity conditions. The SOS pathway mediates ion homeostasis and Na^+ tolerance. A mitogen activated-protein kinase cascade is proposed to mediate osmotic homeostasis. CBF/DREB transcription factors mediate some of the stress protein gene expression in response to secondary stresses.

introduction of *Escherichia coli mtlD* gene, which encodes mannitol-1-phosphate dehydrogenase (Tarcynski *et al.* 1992). It is not normally produced by wild-type tobacco. However, many plants synthesize and accumulate mannitol, sorbitol and polyamines that only partially decrease the amount of inorganic ion accumulation in the cytosol, their protective effect as compatible solutes may be almost sufficient to give marginal growth advantage in plants (Binzel *et al.* 1988). In addition, Rhodes *et al.* (1989) showed that the levels of glycine-betaine (GB) in Poaceae species are correlated with salt-tolerance. Highly tolerant *Spartina* and *Distichlis* accumulated the highest levels, moderately tolerant species accumulate intermediate levels and sensitive species accumulate low levels or no GB.

HUNTING THE TOLERANT RELATIVE: NEW PERSPECTIVE IN SALT RESPONSE UNDER STANDING

Using saline lands for conventional agriculture requires either improving the soil or enhancing the salt tolerance limit of field crops, the majority of which cannot survive with the levels of salinity average prevailing in the fields. These approaches have been applied with variable degree of success involving engineering/reclamation and/or breeding crops for salinity tolerance. Engineering approaches include surface drainage, lining of canals and pumping of ground water, while reclamation of the salt affected soils involves leaching with higher levels of irrigation, use of gypsum or acids, physical removal of salts and growing salt-tolerant plants. The results indicate an expensive and short-term solution to the problems. In some cases, the plants used for rehabilitation were generally grasses that are known to exclude salts, thereby resulting in limited success. Progress in breeding for salt tolerance through gene transfer has been slow, hampered by various factors, e.g. the character is under multigenic control, hence difficult to transfer and not many genes have so far been recognized to play with, not to mention the social acceptance of genetically modified (GM) food. Despite a large amount of efforts have been directed towards increasing the salt tolerance of crops, ranging from

wide-crossing to transgenic, few productive salt-tolerant varieties have been produced (Flowers and Yeo 1995; Flowers 2004; Flowers and Flowers 2005; Witcombe *et al.* 2008).

For this reason, it is perhaps cheaper, easier and may be more successful to domesticate a wild salt-tolerant species or halophytic species than to modify an existing crop to get gainful returns from a saline environment. The utilization of naturally salt tolerant species in agriculture to provide forage, medicinal plants, and aromatic plants and for forestry in saline soils should be the best economic solution presently available (Yeo and Flowers 1980; Flowers and Flowers 2005; Abdelly *et al.* 2006; Khan *et al.* 2009; Ruan *et al.* 2010). Apart from direct use as crops, salt-tolerant species are increasingly being considered for re-vegetation and remediation of salt affected land. Some growing salt-tolerant plants may improve soil properties, such as increasing water conductance or increasing soil fertility (Qadir *et al.* 2008) and some salt marsh plants are capable of extracting heavy metals from sediments accumulating them in their organs (Cambrolle *et al.* 2008).

Thus, the existing levels of salinity in fields require, in the near future, a selection of new salt cultivars or the utilization of the inherent ability of known halophytes to complete their life cycle even under highly saline conditions. In order to achieve these ends, more information is required on the effects of salt and ion relations on the physiological and metabolic processes of plant growth. Numerous studies showed that plants differ greatly in their tolerance of salinity, since their response depends on salt type and level, plant genotype and growth stage (Meneguzzo *et al.* 1999; Houle *et al.* 2001). Salt tolerance is usually assessed as the percent biomass production in saline versus control conditions over a prolonged period of time. For example, after exposure to 200 mM NaCl, a salt-tolerant species such as sugarbeet might have a reduction of only 20% in dry weight, a moderately tolerant species such as cotton might have a 60% reduction, and a sensitive species such as soybean might be dead (Greenway and Munns 1980). Among the cereals, rice (*Oryza sativa*) is the most sensitive and barley (*Hordeum vulgare*) is the most tolerant; bread wheat (*Triti-*

cum aestivum) is moderately tolerant and durum wheat (*Triticum turgidum* ssp. *durum*) is less so. Tall wheatgrass (*Thinopyrum ponticum*, syn. *Agropyron elongatum*) is a halophytic relative of wheat and is one of the most tolerant monocotyledonous species. Moreover, a grain-like species that has been brought to the general attention is the Andean Quinoa (*Chenopodium quinoa*), whose ability to easily stand severe drought and salinity with only little yield reduction has been repeatedly reported (Bosque Sanchez *et al.* 2003; Koyro *et al.* 2008). However, the sustainable use of these plants depends under osmotic and ionic stress on the ability to exhibit a wide range of responses at molecular, cellular and whole plant levels. This includes the synthesis of compatible solutes/osmolytes, specific proteins and radical scavenging mechanisms, ion uptake and compartmentation of injurious ions. Acclimation of these plants to salinity depends also upon activation of cascades of molecular networks involved to stress sensing, signal transduction and the expression of specific stress-related gene and metabolites. The product of these genes may participate in the generation of regulatory molecules such as plant hormones. The deeper understanding and replicability of the physiological and biochemical basis of drought and salt resistance can provide a basis for the cultivation of suitable plants in regions threatened by desertification and water scarcity sustainable culture conditions. Even the drylands could offer tangible economic and ecological opportunities.

Numerous studies have been carried on to identify not only new resistant cultivars and species but also on the plant's ability to germinate, grow and regulate their physiological and metabolic functions over increasing levels of salt stress. Ben Hamed *et al.* (2004) studied the salinity resistance of *Crithmum maritimum* a perennial Apiaceae growing naturally in rocky coasts. The oil extracted from its seeds seems to be convenient for human consumption. The presence of NaCl in the medium imposed a strong restriction in nutrient (K^+ and Ca^{2+}) acquisition, which was due to inhibition of both root intrinsic performance for ion transport and root growth suggesting that salinity restricts *C. maritimum* growth through limitation of mineral nutrient acquisition, rather than osmotic and ionic deleterious effects. In addition, study carried on by Ghars *et al.* (2008) on the halophyte *Thellungiella halophila* and in both wild type and eskimo-1 mutant of the glycophyte *Arabidopsis thaliana*, which differed in their Pro accumulation capacity, showed that *T. halophila* had a great ability to control Na^+ accumulation in shoots. The analysis of the relationship between water and Na^+ contents suggested an apoplastic sodium accumulation in both species; this trait was more pronounced in *A. thaliana* than in *T. halophila*. The better NaCl tolerance in the latter was associated with a better K^+ supply, resulting in higher K^+/Na^+ ratios. It was also noteworthy that, despite highly accumulating Pro, the *A. thaliana* eskimo-1 mutant was the most salt-sensitive species.

Under control conditions, the salt-tolerant *T. halophila* had higher levels of sucrose, fructose, glucose, Pro, citrate, malate, and succinate compared with *Arabidopsis*. However, following salt stress, *T. halophila* showed greater increases in inositol, galactinol, and raffinose and reductions in fumarate, malate, phosphate, and aspartate than did *Arabidopsis* (Gong *et al.* 2005).

Metabolic responses to salt stress are described for two barley (*Hordeum vulgare* L.) cultivars, 'Sahara' and 'Clipper', which differed in salinity tolerance under the experimental conditions used (Widodo *et al.* 2009). Metabolite changes in response to the salt treatment also differed between the two cultivars. 'Clipper' plants had elevated levels of amino acids, including Pro and γ -Aminobutyric acid (GABA), and the polyamine putrescine, consistent with earlier suggestions that such accumulation may be correlated with slower growth and/or leaf necrosis rather than being an adaptive response to salinity. It is suggested that these metabolites may be an indicator of general cellular damage in plants. By contrast, in the more tolerant 'Sahara' plants, the levels of the hexose phosphates, tricarboxylic

acid cycle (TCA cycle), intermediates, and metabolites involved in cellular protection increased in response to salt. These solutes remain unchanged in the more sensitive 'Clipper' plants. It is proposed that these responses in the more tolerant 'Sahara' are involved in cellular protection in the leaves and are involved in the tolerance of 'Sahara' leaves to high Na^+ .

Edelist *et al.* (2009) used semiquantitative RT-PCR to study the expression of eight candidate salt-tolerance genes in leaves of the highly salt-tolerant diploid hybrid species *Helianthus paradoxus* and its salt-sensitive progenitor species *H. annuus* and *H. petiolaris*. Samples were collected after germination and growth under four different treatments: nonsaline (control), near-natural saline, saline with increased K^+ , and saline with decreased Mg^{2+} and Ca^{2+} . Three individuals from three populations per species were used. The hybrid species *H. paradoxus* constitutively under- or overexpressed genes related to potassium and calcium transport (homologues of KT1, KT2, ECA1), suggesting that these genes may contribute to the adaptation of *H. paradoxus* to salinity. In two other genes, variation between populations within species exceeded species level variation. Furthermore, homologues of the potassium transporter HAK8 and of a transcriptional regulator were generally overexpressed in saline treatments, suggesting that these genes are involved in sustained growth under saline conditions in *Helianthus*. Such studies ranged from the promising results from the lab-based physiologists and molecular biologist studies on model plants, to the slower agronomical application on the crop species, where the innovative findings were transferred to improve agriculture.

MECHANISMS OF STRESS RESPONSE IN PLANTS

Seed germination in saline environment

Several studies showed that plants are particularly salt sensitive during seed germination because this process usually occurs in surface soils where soluble salts accumulate as a result of evaporation and capillary rise of water. It should be considered, however, that also halophytic species rarely germinate when high salt concentrations are found in the available water (Duan *et al.* 2004). Consistently, experiments on seed germination rarely provided successful rates of germination or survival as compared to greater vigorous plants. On the other hand, doubts on the correlation between the ability to germinate on salty water and tolerance on mature plants have been repeatedly advocated (Almasouri *et al.* 2001), and indications on retarded germination of halophytes watered with salty water have been described (Duan *et al.* 2004). Song *et al.* (2005) investigated the strategies taken by halophytes such as *Suaeda physophora* (euhalophyte) *Haloxylon ammodendron* (xero-halophyte) and *Haloxylon persicum* (xerophyte) during the seed germination stage to adapt to saline environments in an arid zone. They showed that *H. ammodendron* and *S. physophora* had a higher recovery germination from -3.13 MPa NaCl compared with *H. persicum*. Seeds of all species had no endosperm. More Na^+ was compartmentalized in the seed coats of the two halophytic species compared with that in the xerophyte *H. persicum*. They demonstrated that the effect of NaCl on seed germination was due to both osmotic stress and ion toxicity for the three species. High soil salinity and a high content of Na^+ in seeds may induce more seeds to remain ungerminated in *S. physophora* and *H. ammodendron*. Morphological structure and adaptation to salinity during seed germination may determine the geographical distribution of *H. ammodendron* and *S. physophora* in certain saline regions. Thakur and Sharma (2005) suggested a possible physiological role of Pro for sorghum seed germination in saline media. The authors found low concentration of Pro in dry seeds but its content increased when seeds were germinated in presence of NaCl, suggesting that Pro may be a part of system that keeps the developing

embryonic axis in a dormant state resulting in an important component of germination. Wang *et al.* (2009) investigated the physiological behaviours and antioxidant responses of *Medicago sativa*, *Melilotus officinalis* and *Astragalus adsurgens* to saline environment during seed germination stage, showing that at 300 mM NaCl treatments, the final germination percentage of *M. officinalis* was much higher than that of *M. sativa* and of *A. adsurgens* and the initiation of germination process of *A. adsurgens* was 5 days later than the others. Moreover, after being treated in 300 mM NaCl, much weaker CAT activity in seed of *M. officinalis*, POX activity in seed of *A. adsurgens* and GR activity in seed of *M. sativa* were found in the controls and salt treatments, suggesting that the oxidative stress could be an influential component of salt stresses on plant seeds during seed germination stage.

On seeds of chickpea (*Cicer arietinum* L. cv. 'PBG-1') a gradual decrease in germination percentage was observed with increasing NaCl concentration, and a complete inhibition was detected at 200 mM NaCl (Kaur *et al.* 1998). This decrease was concomitant with a reduction of both amylase 1 and amylase 2 activities in cotyledons under salt stress. These findings were confirmed by Sidari *et al.* (2008), who found an activity inhibition of these enzymes in a dose-dependent manner in *Lens culinaris*. Soltani *et al.* (2006) studied the effects of salinity and drought on germination stage in two cultivars of wheat (*Triticum aestivum* L.) with the objective to identify the main elements of sensitivity. The results showed that seedling growth, fraction of seed reserve utilization and weight of mobilized seed reserve decreased with increasing drought and salt intensity, but these stresses had no effect on the conversion efficiency of utilized seed reserve to seedling tissue. It was concluded that the sensitive component of seedling growth is the weight of mobilized seed reserve. Muscolo *et al.* (2007) and Sidari *et al.* (2008) studied the salt resistance of lentil, a legume considered to be salt sensitive, evaluating responses to salt stress (0, 50, 100, 150 and 200 mM NaCl) of four lentil genotypes (three landraces, 'Castelluccio di Norcia', 'Pantelleria' and 'Ustica' and a commercial variety, 'Eston'). In particular, 'Pantelleria' and 'Ustica' are native of the homonymous small islands close to Sicily (Southern Italy); 'Castelluccio di Norcia' of Umbria (Central Italy), and 'Eston' is a Canadian commercial variety recently introduced in Italy. The different cultivars were assessed in terms of seed germination efficiency (germination percentage, root length, dry and fresh weight and water uptake). Increasing of NaCl concentrations reduced the germination percentage, the growth parameters and the relative water content; the entity of these inhibitory effects differed depending on tested genotypes. The results showed that the detrimental effects were smaller in 'Ustica' and 'Pantelleria' landraces as compared to 'Castelluccio' and, at minor extent, to 'Eston', particularly at the greatest concentration of NaCl. The four lentil cultivars, differing in salt sensitivity, were also examined for osmolyte contents and activities of α -amylase, β -amylase and α -glucosidase, enzymes involved in seed germination. The inhibitory effects of NaCl differed, depending on the genotype considered. 'Pantelleria' and 'Ustica' seeds, in response to salt stress, accumulated the highest Pro and total soluble sugar concentrations which improved their water status and the enzyme activities involved in the germination process. Consistently, the authors suggested the increase of osmolyte accumulation in seeds as a possible strategy for the improvement of salt stress tolerance in lentils. The synthesis of these compounds occurs at the expense of plant growth but may allow the plant to survive in presence of high external salt concentrations, drought and low temperature. Muscolo and Sidari (2008) studied seed germination and the activities of the main enzymes involved in reserve utilization (glyoxylate cycle enzymes), under salinity and drought stress. The results showed that both seed germination and enzyme activities decreased with increasing PEG (polyethylene glycol), NaCl and seawater concentrations. Seawater appears to be the

least toxic salinizing agent on *Pinus* (*Pinus pinea*, L) seed germination, indicating that the germination was influenced by the concentrations and even more by the nature and interactions of the ions present in the solutions that affect the enzymes involved in seed mobilization reserve. This finding was in accordance with previous report of Lin and Kao (1995) showing that salt and osmotic stresses limit the mobilization of reserves in several species.

Easton and Kleindorfer (2009) investigated the effects of salinity on germination of 12 Australian species of the plant genus *Frankenia*. They used saline solutions that corresponded to the average soil-water salinity concentrations in the arid zones of inland Australia and consisted of 10mM calcium chloride, 30 mM magnesium sulphate, and 450 mM sodium chloride. The aims of the study were: (1) to investigate germination rates and germination success of *Frankenia* seeds exposed to four salinity levels (0, 10, 20, 30‰), (2) to test for possible interaction effects between seed mass, germination, and salinity, and (3) to examine the effect of salinity levels on the inhibition of germination and/or seed damage. The results showed that *Frankenia* species with larger seeds had higher germination rates and germination success for high salinity levels, but several of them did not germinate well at any salinity level. Finally, no seeds were adversely affected by exposure to high salinity levels prior germination. These results provide indirect evidence that natural selection in some Australian *Frankenia* species to develop larger seeds (consequence of the reduction in ovule number) has facilitated their establishment and reproduction under conditions that were less favorable for plants with smaller-seeds.

Jafarzadeh and Aliasgharzad (2007) investigated on the effect of water salinity levels and two salt compositions (NaCl alone and mixture of MgSO₄ + NaCl + Na₂SO₄ + CaCl₂) on germination of four sugar beet cultivars. Statistical analysis revealed that germination was significantly affected by salt composition, cultivars and salinity levels. Regardless of salt composition, seed germination was significantly affected by the irrigation water with EC up to 8 dS/m and 4 dS/m, respectively. The adverse effect of salinity of the irrigation water on seed germination was higher for NaCl alone than for the salt mixture, which refers to lower salt stress in field conditions with natural salt composition. In contrast, Kaymakanova (2009) studied the response of three bean cultivars (*Phaseolus vulgaris* L.) to equimolar NaCl and Na₂SO₄ salinity at germination and early seedling growth to evaluate the effect of monosaline iso-molar solutions of NaCl and Na₂SO₄ on germination. Seeds were germinated and grown in Petri plate on filter paper with solution of the respective treatment and incubated at 25°C in a thermostat. The author demonstrated that all treated cultivars registered decrease in the percentage of germination, seedlings growth and respiration rate. The cultivars were inhibited stronger by Na₂SO₄ than NaCl treatment, suggesting that single ions may differ for their toxic effects decreasing the germination in different type of salinity.

An opportunity to improve the germination in presence of salinity could be seed pretreatments, as reported by Meot-Duros and Magné (2008) on the halophyte *Crithmum maritimum* L. Seeds undergoing salt stress did not germinate but they recovered rapidly upon transfer to distilled water and the recovery was higher after a low salinity pretreatment. Chemical treatments resulted in differential effects on seed germination. Known dormancy breakers, such as potassium nitrate and thiourea, had no effect on sea fennel seed germination. Conversely, L-ascorbic acid (40 or 60 mM) and ethanol (96%) significantly improved germination rate by 10, 30 and 30%, respectively. Pretreatment of seeds with L-ascorbic acid at 40 mM was shown to alleviate the negative effects of low NaCl concentration on germination. These findings indicate that the application of ascorbic acid may be used to improve sea fennel seed germination.

Mechanisms of ion homeostasis: Maintaining growth under impaired uptake

Studies carried out on seedlings demonstrated that salinity reduces plant growth and enhances senescence of mature leaves, resulting in a reduction in functional leaf area. A sudden increase in salinity causes a water loss of leaf cells due to the osmotic effect of the salt around the roots. This effect is transient and within hours, cells regain their original volume and turgor owing to osmotic adjustment, but despite this, cell elongation rates are reduced (da Silva *et al.* 2008; Wu and Zou 2009) and consequently plant growth.

Numerous works (Shalata and Tal 1998; Heidari 2009) have demonstrated the importance of osmolyte production to increase salinity tolerance in plants. In order to maintain low cytosolic Na⁺, and cytosolic K⁺ concentrations within narrow limits (100–150 mM) across a broad range of NaCl external and vacuolar concentrations, it is essential that other solutes be accumulated in the cytoplasm to keep this compartment in osmotic balance with the external medium and vacuole. These solutes are osmolytes, non-toxic and “compatible” with cytoplasmic enzymes over wide concentration ranges. A number of such solutes have been identified, their pathways of synthesis elucidated, and progress has been done in isolating genes encoding key enzymes of their biosynthetic pathways.

Muscolo *et al.* (2003a, 2003b), investigated the effects of NaCl salinity on growth and metabolism of kikuyu grass (*Pennisetum clandestinum* Hoechst), showing a tolerance to salinity of this grass up to 100 mM NaCl. Higher salinity levels affected nutritive properties of kikuyu and root growth more than shoots. In plants exposed to highest salt conditions, a lower activity of the enzymes involved in the glycolytic pathway caused an accumulation of hexoses, indicating the importance of these osmolytes for plant salt resistance. This was also demonstrated by Karimi *et al.* (2005) who evaluated the effects of NaCl on growth, water relations, osmolytes and ion content in *Kochia prostrata*, a salt tolerant species with an optimal growth up to 150 mM NaCl. Among the potential mechanisms of salt tolerance adopted by this plant were supposed a balance among ion accumulation and production of GB, Pro, soluble sugars to maintain osmotic pressure in this compartment. These findings were also confirmed by Ueda *et al.* (2007) that found an accumulation of Pro in response to salinity in barley plants. They demonstrated, by immunohistochemical analysis, that Pro transporter (HvProT) was highly expressed in the apical region of barley roots under salt stress, while free Pro was more accumulated in the root basal region. Moreover, salt stress increased Pro and hydroxyproline contents in the cell wall fraction of the root apical region, suggesting an increment of Pro utilization. Expression of the genes encoding cell wall proteins (Pro-rich and extensin proteins) and cellulose synthase was induced in barley roots by salt stress.

On this subject, Perica *et al.* (2008) studied the effect of salinity on olive (*Olea europea* L.) trees (generally considered as moderately tree tolerant to salinity). They determined the effect of NaCl on shoot and root growth, dry matter allocation, leaf Na⁺ and K⁺ concentration, electrolyte (EL) and K⁺ leakage (KL). Seven olive cultivars of different origins were grown in a nutrient solution containing 0, 33, 66, 100 or 166 mM NaCl, for three months. The general effect of salinity was linear and a quadratic decrease of plant growth parameters was observed. Different responses of the tested cultivars to the applied levels of salinity were found for stem dry weight, shoot length and leaf number. As salinity increased, growth of ‘Manzanillo’ declined sharply, whereas ‘Frantoio’ was the most salt tolerant cultivar. Allometric analysis showed that biomass allocation under salinity stress was similar in all cultivars, but the slope between shoot weight and total plant weight decreased when salinity increased. Since the higher allocation in roots was not found, it seems that salinity only slowed the above ground plant canopy growth. Sodium concentration in

leaves of all cultivars increased concomitantly with salinity and the highest content was reached when the NaCl concentration of nutrient solution raised from 100 to 166 mM. Significant differences among genotypes were found in leaf Na⁺ and K⁺ content and Na⁺/K⁺ ratio, but they were not related to the growth rate. Generally, ‘Frantoio’ and ‘Oblica’ accumulated less Na⁺ and were able to maintain lower Na⁺/K⁺ ratios as compared to the other genotypes. Electrolyte and K⁺ leakage increased linearly with increasing salinity and the magnitude of the response depended upon the olive cultivars. In saline conditions, nutrient imbalances can result through various ways: from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant or may be caused by physiological inactivation of a given nutrient (such as K) resulting in an increase in the plant's internal requirement for that essential element. Alleviating the opposing effects of salinity on the plant growth could be possible by modification of nutrients supply. Adverse salinity effects on plant growth and tolerance to salinity can be altered by mineral nutrition (Grattan and Grieve 1994; Ebert *et al.* 2002). It is in fact well known that addition supply of Ca or NO₃ to salt stressed plants improves their tolerance to salinity (Ebert *et al.* 2002). Tabatabaei and Fakhrzad (2008) showed that the effect of KNO₃ application on perennial ryegrass increased saline tolerance suggesting that 10 mM KNO₃ reduced Cl concentration, increased Pro and K/Na ratio improving the tolerance to salinity.

Antioxidants: the healthy side of the stress

At high salinity, salts can build up in leaves to excessive levels and exert a direct toxic effect on photosynthetic processes in the chloroplast. The reduced rate of photosynthesis increases the formation of ROS and therein the activity of enzymes that detoxify these species (Rawat and Banerjee 1998; Redondo-Gómez *et al.* 2007). One of the biochemical changes occurring when plants are subjected to harmful stress conditions is the accumulation of ROS (Smirnoff 1993), which are inevitable by-products of normal cell metabolism. The chloroplasts and mitochondria of plant cells are major intracellular generators of ROS. These cytotoxic oxygen species are highly reactive and in the absence of any protective mechanism they can seriously disrupt normal metabolism through oxidative damage resulting in lipid peroxidation and consequent membrane injury, protein degradation, enzyme inactivation, pigment bleaching and disruption of DNA strands. Antioxidative enzymes are the most important components in the scavenging system of ROS (Moloi *et al.* 2008).

In kikuyu grass the response of the antioxidant system to long term (15 d) salt stress was studied (Muscolo *et al.* 2003b). The results showed an up regulation of APX, POX and GR enzymes suggesting that for kikuyu grass the resistance to salt stress (up to 100 mM) appears to be related to the increased activity of the main antioxidant enzymes.

Khosravinejad *et al.* (2008) investigated antioxidant activities of SOD, CAT, APX and POX in two barley cultivars under increasing concentrations of NaCl for 3 days. In general, the activities of antioxidant enzymes were increased by salinization in both roots and shoots, but the increase was more consistent in roots, directly dealing with the salt in the soil. Among the antioxidant enzymes, CAT activity was enhanced the most significantly. Studies on wheat confirmed a direct relationship between salt resistance and increase in anti-oxidative enzyme activities (Esfandiari *et al.* 2007).

Heidari and Mesri (2008) confirmed these findings in three cultivars of wheat. In wheat under salinity stress antioxidant enzymes and compatible solutes helped to plant adaptation suggesting a positive correlation between Na⁺ concentration in the shoots and the antioxidant enzyme activities and compatible solutes in the leaves. Aghaei *et al.* (2009) studied the response of potato to salt stress, antioxidant enzyme activities and ion content for a sensitive

(‘Concord’) and tolerant (‘Kennebec’) cultivars. These studies established that enzyme activities in ‘Concord’ shoots are inversely related to the NaCl concentration, whereas those in ‘Kennebec’ do not show a dose dependency, which is also the case for the roots of both cultivars. These findings suggest that an increase in activity of antioxidant enzymes, such as APX, CAT and GR, can contribute to salt tolerance in ‘Kennebec’, a salt resistant cultivar of potato. Kartashov *et al.* (2008) studied the role of antioxidant systems in wild plant adaptation to salt stress. Wild plants differing in the strategies of adaptation to salinity were grown for six weeks in the phytotron and then subjected to salt stress (100 mM NaCl, 24 h). Independently of the level of constitutive salt tolerance, plants of all species tested accumulated sodium ions under salinity conditions but differed in their capability of stress-dependent Pro accumulation and SOD and POX activities. Pro-accumulating species were found among both halophytes (*Artemisia lerchiana* and *Thellungiella halophila*) and glycophytes (*Plantago major* and *Mycelis muralis*). The high activities of ionically-bound and covalently bound peroxidases were characteristic of *Th. halophila* plants. High constitutive and stress-induced SOD activities were, as a rule, characteristic of glycophytes with the low constitutive Pro level: *Geum urbanum* and *Thalictrum aquilegifolium*. Thus, a negative correlation was found between Pro content and SOD activity in wild species tested; it was especially bright in the halophyte *Th. halophila* and glycophyte *G. urbanum*. Extremely high constitutive and stress-induced levels of Pro and POX activity in *Th. halophila* may compensate the low SOD activity in this plant, contributing to its salt resistance. These findings suggest that high SOD activity is not an obligatory trait of species salt tolerant, while high POX activity could be correlated to salt stress tolerance independently from SOD activity. Sakr and Arafa (2009) investigated the role of some applied antioxidants (spermine 10 mg L⁻¹ and ascorbic acid 200 mg L⁻¹) in counteracting the harmful effect of soil salinity stress (10.1 or 14.6 dS m⁻¹) on canola plants. The application of antioxidants increased each of photosynthetic pigments, Pro, soluble sugar, N, K and P contents, while decreased Na⁺ and Cl⁻ contents in canola plants under both soil salt stress during two growing seasons. These findings evidence that antioxidant application could counteract the harmful effect of salt soil stress on growth, yield and biochemical constituents of canola plant confirming the important role of the antioxidant in inducing salinity resistance. The protective role of antioxidants was investigated by Rubio *et al.* (2009) in *Lotus japonicus* exposed to two salinization protocols: S1 (150 mM NaCl for 7 d) and S2 (50, 100 and 150 mM NaCl, each concentration for 6 d). Several markers of salt stress were measured and the expression of antioxidant genes was analyzed using quantitative reverse transcription–polymerase chain reaction and, in some cases, immunoblots and enzyme activity assays. Leaves of S1 plants suffered from mild osmotic stress, accumulated Pro but no Na⁺, and showed induction of many SOD and glutathione peroxidase (GSH-Px) genes. Leaves of S2 plants showed increases in Na⁺ and Ca²⁺, decrease in K⁺, and accumulation of Pro and malondialdehyde. In leaves and roots of S1 and S2 plants, the mRNA, protein and activity levels of the ascorbate-glutathione enzymes remained constant, with a few exceptions. Notably, there was consistent up-regulation of the gene encoding cytosolic dehydroascorbate reductase, and this was possibly related to its role in ascorbate recycling in the apoplast. The overall results indicate that *L. japonicus* is more tolerant to salt stress than other legumes, which can be attributed to the capacity of the plant to prevent Na⁺ reaching the shoot and to activate antioxidant defenses. Peng *et al.* (2009) studied the effect of drought and salinity stress on the seedlings of the somatic hybrid wheat cv. ‘Shanrong No. 3 (SR3)’ and its parent bread wheat cv. ‘Jinan 177 (JN177)’ was investigated using two-dimensional gel electrophoresis and mass spectrometry. Of a set of 93 (root) and 65 (leaf) differentially expressed proteins (DEPs), 34 (root) and six (leaf) DEPs

were cultivar-specific. The remaining DEPs were salinity/drought stress-responsive but not cultivar-specific. Many of the DEPs were expressed under both drought and salinity stresses. The amounts of stress-responsive DEPs between ‘SR3’ and ‘JN177’ were almost equivalent, whereas only some of these DEPs were shared by the two cultivars. Overall, the number of salinity-responsive DEPs was greater than the number of drought-responsive DEPs, and most of the drought-responsive DEPs also responded to salinity. There are both similarities and differences in the responses of wheat to salinity and drought. A parallel transcriptomics analysis showed that the correlation between transcriptional and translational patterns of DEPs was poor. The enhanced drought/salinity tolerance of ‘SR3’ appears to be governed by a superior capacity for osmotic and ionic homeostasis, a more efficient removal of toxic by-products, and ultimately a better potential for growth recovery.

ROS detoxifying mechanisms are present in all plants and these biochemical responses to salinity are often similar to responses induced by other environmental stress, for this may rely on common stress-tolerance pathways (Munns and Tester 2008).

WHERE SALT GETS IN: ROLE OF THE ROOT

Little work has been carried out on the improvement of roots with regard to either salt or water stress. Roots might seem the part of the plant most vulnerable as they are directly exposed to salt or to drying soil, but they are surprisingly robust, their growth rate is not as affected as that of shoots.

Root systems are known to show a high degree of plasticity in their development in response to local heterogeneity of the soil. On the level of the individual root and the entire root system, various morphological parameters such as length, section, surface area, root hairs are used as potential indicator of root plasticity in response to environmental conditions and change. Responses of biomass allocation patterns and structural traits such as specific root length, root tissue density and root diameter distribution, are associated with acquisition capacities for below-ground resources and respond to stresses.

Cachorro *et al.* (1995) evaluated the effect of 80 mM NaCl on the structure and ultrastructure of root cells of *Phaseolus vulgaris* plants. Their results showed that roots of plants treated with NaCl were shorter and had less secondary roots than control plants. In control plants, epidermal cells were isodiametric and uniformly placed forming a thin layer, whereas in stressed plants, the shape and disposition of epidermal cells was less regular. The cortical cells of control plant were round-shaped and distributed allowing large and well defined intercellular spaces, whereas stressed plants presented irregular cells, which were interdigitated, thus decreasing the volume of the intercellular spaces. Presence of 80 mM NaCl resulted in significant changes in root anatomy.

Changes in root system were also observed in kikuyu (*Pennisetum clandestinum* Hoechst) seedlings grown in Hoagland nutrient solution with different salt concentrations (Muscolo *et al.* 2004). Meristematic apex of kikuyu roots, in presence of increasing salt concentrations, showed a mean growth, similar to that of control, whereas a significant reduction in root tips, was evident. The cross sections of the primary structure of kikuyu grass roots exposed to 50 and 100 mM NaCl did not show significant changes in the cortex growth and stele development; in contrast 200 mM NaCl caused a significant reduction in the relative volume of the endodermis around the central cylinder, a thickness of the Casparian band and an increase in the number and diameter of root metaxylem vessels. These anatomical modifications may increase the mechanical resistance and decrease the root permeability to avoid the toxic effects of the excess of ions.

Root hair development is controlled by environmental signals. Wang *et al.* (2008) studied root hair plasticity,

growth and their physiological role in response to salt stress in *Arabidopsis thaliana*. They evidenced that root epidermal cell types and root hair development are highly regulated by salt stress. Root hair length and density decreased significantly in a dose-dependent manner on both primary roots and junction sites between roots and shoots. The root hair growth and development were sensitive to inhibition by ions but not to osmotic stress. High salinity also altered anatomical structure of roots, leading to a decrease in cell number in N positions and enlargement of the cells. Moreover, analysis of the SOS mutants indicated that salt induced root hair response is caused by ion disequilibrium and it may be an adaptive mechanism to reduce an excessive ion uptake. It is well shown that genes WER, GL3, EGL3, CPC, and GL2 might be involved in cell specification of root epidermis in stressed plants. Taken together, these data suggest that salt-induced root hair plasticity represents a coordinated strategy for early stress avoidance and tolerance as well as a morphological sign of stress adaptation. The effect of salinity on primary root growth has been extensively studied. However, how salinity affects lateral root development and its underlying molecular mechanisms is still unclear.

Wang *et al.* (2009) showed that high salt exposure suppressed lateral root initiation and organogenesis, resulting in the abortion of lateral root development; in contrast, salt stress markedly promoted lateral root elongation suggesting auxin plays an important role in the modulation of root system architecture mediating responses to a broad range of external signals. Histochemical staining showed that the quantity of auxin and its patterning in roots were both greatly altered by exposure to high concentrations of salt, as compared with those found in the untreated control. Physiological experiments using transport inhibitors and genetic analysis revealed that the auxin transport pathway is important for salt-induced root development. These results demonstrate that auxin transport activities are required for remodeling lateral root formation and elongation and for adaptive root system development under salt stress.

In summary, roots do most of the work in protecting the plant from excessive uptake of salts, and filter out most of the salt in the soil while taking up water. Even so, there are mechanisms for coping with the continuous delivery of relatively small amounts of salt that arrive in the leaves, the most important being the cellular compartmentalisation of salts in the vacuoles of the mesophyll cells. This strategy allows plants to minimize or delay the toxic effects of high concentrations of ions on important and sensitive cytoplasmic processes. The rate at which leaves die is the rate at which salts accumulate to toxic levels, so genotypes that have poor control of the rate at which salt arrives in leaves, or a poor ability to sequester that salt in cell vacuoles, have a greater rate of leaf death.

NEW DIRECTIONS: SHIFTING THE SALINITY THRESHOLD OR FLATTENING THE DECAY SLOPE?

Crop salt tolerance is generally assessed as the relative yield response to increasing root zone salinity, expressed as soil (ECe) or irrigation water (ECw) electrical conductivity. Alternatively, the dynamic process of salt accumulation into the shoot relative to the shoot biomass has also been considered as a tolerance index. These relationships are graphically represented by two intersecting linear regions, which identify (1) a specific threshold tolerance, at which yield begins to decrease, and (2) a declining region, which defines the yield reduction rate. Although the salinity threshold is intuitively a critical parameter for establishing plant salt tolerance, in a recent work Maggio *et al.* (2007) focused on the physiological modifications that may occur in the plant at salinity higher than the so-called tolerance threshold. For this purpose, hydroponically grown tomato plants were exposed to eight different salinity levels (EC = 2.5, non-salinized control; 4.2; 6.0; 7.8; 9.6; 11.4; 13.2; 15.0

dSm⁻¹). It was identified a specific EC value (approximately 9.6 dS m⁻¹) at which a sharp increase of the shoot and root ABA levels coincided with (1) a decreased sensitivity of stomatal response to ABA; (2) a different partitioning of Na⁺ ions between young and mature leaves; (3) a remarkable increase of the root-to-shoot ratio. Although the bilinear response after the specific salinity tolerance threshold has been reported by other authors (Dalton *et al.* 1997), the physiological significance of this slope change has never been functionally analysed in terms of salinity tolerance. Several authors have suggested that morphological root and shoot traits can play an important role in plant stress adaptation. Dalton *et al.* (2000) indicated that a reduced root relatively to the shoot development may increase the tomato salinity tolerance by delaying the onset of a critical level of ion accumulation/toxicity into the shoot. A systematic study on the contribution of these traits to salinity tolerance in specific cultural contexts has never been pursued. In addition to grafting techniques that may involve uncontrollable physiological disturbances, root habits and characteristics could be modified via genetic engineering since genetic determinants that affect root length, lateral root development and root hair formation have been thoroughly characterized in cereals (Hochholdinger *et al.* 2004). This hypothesis can be also tested vs. the large collections of root mutants available in model species and, to a less extent, in tomato or other species. In this respect, the possibility of integrating the output of biophysical models with biotechnological tools should be further considered.

STRATEGIES TOWARD MULTI-STRESS TOLERANCE

Halophytic species are often able to stand different kind of stresses, ranging from drought and salinity to freezing or heat (Flowers *et al.* 1986; Glenn *et al.* 1999). These plants are characterized by morpho-physiological traits (eg. Reduced growth, lower photosynthetic rates, etc.) and response mechanisms (eg. higher control of ABA biosynthesis), that reduce the shock imposed by the stress and allow a quick recover.

Numerous studies (Flowers *et al.* 1977; Glenn *et al.* 1999; Benlloch-González *et al.* 2005; Flowers and Colmer 2008; Ruan and Teixeira da Silva 2011) have addressed the metabolic traits of the halophytes and salt-tolerant plants. Halophyte species demonstrate differing levels of salt tolerance. Understanding interspecific variation to salinity levels is of value from both the scientific perspective, which includes the identification of traits associated with salinity tolerance, as well as from an applied perspective, which includes identifying plant species for specific salinity restoration and remediation projects.

Stetsenko *et al.* (2009) evaluated the content of free and conjugated polyamines (PA) in leaves of secondary shoots and in roots of the facultative halophyte *Mesembryanthemum crystallinum* L. under salinity. PA in plants can be in free or bound form (with low-molecular-weight compounds and macromolecules) (Kuznetsov *et al.* 2006, 2007). The most important characteristic of PA conjugates with phenolic acids, during plant adaptation to stress, is their antioxidant activity. Then the formation of these PA conjugates in plants may neutralize damaging effects under stress conditions. However, the formation of PA conjugates with phenolic compounds under is dependent on plant species, as well as their content of PA and phenolic substances. Martin-Tanguy (2001) evidenced an organ specificity for the content of free and conjugated forms of PA, as well as an active role in adaptation of *Mesembryanthemum crystallinum* to salinity shock. Li *et al.* (2010) studied the interactive effects of various salt and alkali stresses on a halophyte *Spartina alterniflora* (Poaceae). The experiment consisted of six levels of salinity (100, 200, 300, 400, 500, and 600 mM) in each of six pH levels: A (pH 7.1 ± 0.02), B (pH 8.1 ± 0.17), C (pH 8.8 ± 0.14), D (pH 9.8 ± 0.14), E (pH 10.4 ± 0.08), and F (pH 10.8 ± 0.10). The survival rate, RGR, tiller rate,

rhizome number, leaf Chl content, root activity, electrolyte leakage rate (ELR), and Pro, soluble carbohydrates, Na^+ , K^+ contents were determined. The results showed that *S. alterniflora* was able of surviving all treatments under low pH ($\text{pH} \leq 8.30$) regardless of the salinity levels. However, high pH in conjunction with salinity sharply reduced survival rate. The interactive effects of salinity and high pH on RGR, tiller rate, rhizome number, leaf chlorophyll content, and relative root activity were additive. Moreover, ELR and Na^+/K^+ ratio increased with increasing salinity and pH. The content of Na^+ increased, while K^+ decreased with increasing salinity and pH, suggesting that the competitive inhibition between Na^+ and K^+ was in favor of Na^+ . The content of both Pro and soluble carbohydrates increased with salinity and pH, suggesting that alkali stress may also induce accumulation of these organic solutes. The deleterious effects of high pH or salinity alone were significantly less than those of combined high pH and salinity. For salt-alkali mixed stress, it was concluded that reciprocal enhancement between salt and alkali stress is a characteristic feature. Through multiple linear regressions a strong correlations between all physiological indices and the three stress factors were found, showing that the effects of the three stress factors on the physiological indices were different in magnitude. Even if salinity is the dominant factor, and pH and buffer capacity are secondary, the combined action of salinity, pH, and buffer capacity should be considered when evaluating the strength of salt-alkali mixed stress.

Numerous studies (Khan *et al.* 2000, 2002) have been carried on to identify new cultivars with resistance to salinity and analogies with metabolism of resistant cultivars or halophytes.

Effects of long-term sodium chloride salinity (100 and 200 mM NaCl; $\text{ECe} = 6.85$ and 12.3 dS m^{-1}) were studied in tolerant and susceptible wheat genotypes (Sairam *et al.* 2005). NaCl decreased relative water content, chlorophyll content, membrane stability index (MSI) and ascorbic acid (AA) content, and increased the contents of hydrogen peroxide, thiobarbituric acid reactive substances (TBARS), and activities of SOD, APX and GR. Tolerant wheat genotypes showed lowest decline in RWC, Chl, MSI and AA content, lowest increase in H_2O_2 and TBARS contents and higher increase in SOD and its isozymes, APX and GR, while sensitive genotypes showed the highest decrease in AA content, highest increase in H_2O_2 and TBARS contents and smallest increase in activities of antioxidant enzymes. From the above results it can be concluded that both constitutive as well as salt induced increase in antioxidant enzymes activities are important for providing protection against ROS and the efficiency of the antioxidant response actually decides the level of tolerance of a plant to salinity or to abiotic stress. Koca *et al.* (2007) studied differences in growth parameters, lipid peroxidation, antioxidative enzyme activities and Pro accumulation in order to put forward the relative tolerance or sensitivity of two different sesame cultivars. Results indicated that both parameters were different under salinity, according to the cultivar's ability in coping oxidative stress. Constitutive levels of antioxidative enzyme activities were almost the same between the cultivars; however, in the cv. 'Cumhuri', the antioxidative enzyme activities were induced more efficiently when subjected to salt stress. Study of Gapińska and coworkers (2008) on tomato plants suggested that the oxidative stress appeared earlier and more intensively in the roots than in the leaves of the treated tomato plants. In conclusion, enhanced activities of total SOD, CuZn-SOD, GSH-Px and glutathione *S*-transferase (GST) in NaCl-treated-plants indicated their involvement in early and late defense systems against ROS induced by salinity stress.

SUMMARY POINTS

- Plant responses to salinity depend on salt type and level, plant genotype and growth stage.
- Plant adaptations to salinity depend on ROS detoxifying

mechanisms that increase the ability to maintain growth under stress conditions. The efficiency of the antioxidant response actually decides the level of tolerance of a plant to salinity.

- The balance between ion accumulations and osmolyte production is important to maintain internal osmotic pressure increasing the ability to keep up plant growth. Osmotic tolerance is evident mainly by the production of new leaves.
- Roots play a fundamental role in protecting the plants from excessive uptake of salts and they filter out most of the salt in the soil while taking up water. This strategy allows plants to minimize or delay the toxic effects of high concentrations of salts, so genotypes with a poor ability to sequester salts have a greater rate of leaf death. Auxin plays a key role in shaping plant architecture and it mediates responses to a broad range of external signals. Stress can impact on various aspects of auxin homeostasis and auxin transport activities are important for adaptive root system development under salt stress.
- Possible approaches to improve productivity under salinity stress conditions require a better understanding of the mechanisms involved in the response to salt stress. The linkage of transcriptional and biochemical responses with regulatory mechanisms may be crucial to determine salinity tolerance in plants. The link with functional genomics may lead to the identification of candidate genes as tools to further elucidate the mechanisms involved in the efficiency of rhizobial symbiosis and its adaptation to abiotic constraints. The investigation of changes in morphological parameters and in root architecture can represent a valid methodological approach in the evaluation of the effects of salinity on plant growth and may favour the identification of root adaptive traits for genetic adaptation of plants to environmental salt stress. More interdisciplinary work is needed at the field level with agronomists and producers and interactions with physiologists and genomists should be emphasized and the cooperation between bacteriologists and plant breeders has to be stimulated.

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