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Overcoming Salinity Barriers to Crop Production Using Traditional Methods

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Salinity is a major problem in arid and semi-arid regions, where irrigation is essential for crop production. Major sources of salinity in these regions are salt-rich irrigation water and improper irrigation management. The effects of salinity on crops include inhibition of growth and production, and ultimately, death. There are two main approaches to alleviating the adverse effects of salinity on agricultural crops: (i) development of salt-tolerant cultivars by screening, conventional breeding or genetic engineering, and (ii) the traditional approach dealing with treatments and management of the soil, plants, irrigation water, and plant environment. The success of the first approach is limited under commercial growing conditions, because salt-tolerance traits in plants are complex. The present paper reviews, analyzes, and discusses the following traditional approaches: (i) improving the plant environment, (ii) exploiting interactions between plant roots and bacteria and fungi, and (iii) treating the plant directly. With respect to improving the plant environment, we review the possibilities of decreasing salt content and concentration and improving the nutrient composition and concentration in the root zone, and controlling the plant's aerial environment. The interactions between salt-tolerant bacteria or mycorrhizal fungi and root systems, and their effects on salt-tolerance, are demonstrated and discussed. Discussed treatments aimed at alleviating salinity hazard by treating the plant directly include priming of seeds and young seedlings, using proper seed size, grafting onto tolerant rootstocks, applying non-enzymatic antioxidants, plant growth regulators or compatible solutes, and foliar application of nutrients. It can be concluded from the present review that the traditional approaches provide promising means for alleviating the adverse effects of salinity on agricultural crops.

Keywords sodium, leaching, mycorrhiza, compatible solute, antioxidant, grafting, growth regulator

I. INTRODUCTION

Salinity is a major abiotic stress responsible for reduced crop production in many of the world's regions. According to an FAO survey (2008), it is expected that over 800 million ha will be affected by salinity in the near future, making it a major constraint to food production for a steadily increasing population. Salinity occurs mainly in arid and semi-arid regions, where evapotranspiration exceeds annual precipitation and irrigation is the essential means for crop production. Currently, at least 20% of the world's irrigated land is salt-affected and/or irrigated with water containing elevated salt levels (Qadir *et al.,* 2008), and it has been estimated that an additional 2 million ha of agricultural land are affected by salinity every year (Kalaji and Pietkiewica, 1993). This increased salinization of arable land is expected to result in a 50% loss of arable land by the middle of the 21st century (Wang *et al.,* 2007). Man-induced salinity began with the irrigated cultivation of arid land along river banks. Written documentation of the existence of salty land can be dated back to the alluvial plains between the Tigris and Euphrates rivers during the ancient Sumerian and Akkadian periods (Hillel, 2005).

Soil salinity can also be a consequence of natural causes, such as the following: (i) weathering of parent rocks and minerals in the soil, which releases various ions (e.g., Na, Ca, K and Mg, sulfates and carbonates) to the soil solution (Moreira-Nordemann, 1984; Szabolcs, 1989); (ii) seawater intrusion into coastal areas leading to increased salinity levels in the soil and channel water, which may be the major factor in the marked decreases in crop production in these areas (Mahajan and Tuteja, 2005; Kotera *et al.,* 2008); (iii) rainwater for example, containing 50 mg L^{-1} NaCl (Munns and Tester, 2008) can result in the precipitation of 250 kg NaCl per ha for every 500 mm of annual rainfall; (iv) wind-borne materials from lake or land surfaces. Nevertheless, the more significant proportion of saline soils is attributed to intensive agricultural cultivation (FAO, 2008). The removal of natural perennial vegetation and its replacement with annual agricultural crops (Manchanda and Garg, 2008) was likely the first factor in man-induced salinity. Use of salt-rich irrigation

water is undoubtedly one of the foremost factors responsible for soil salinity. In addition, improper irrigation management, which might be responsible for a rise in the water table—known as secondary salinization—is an important contributor to soil salinity.

The main salinity effect on crops is inhibition of plant growth and development, and death under extreme salinity levels. Salinity-induced growth inhibition has been shown for all plant organs that are responsible for development of final yield. For example, salinity reduced the number of pods and the rate and duration of grain-filling in soybean, leading to a concomitant decrease in grain weight (Ghassemi-Golezani *et al.,* 2009); in various oat lines, a reduction in grain yield was due to reduced grain number and mean grain weight (Zhao *et al.,* 2009); in durum wheat and barley, both grain number and straw weight were reduced (Katerji *et al.,* 2009); in tomato, the fruit was the most salinity-sensitive organ (Reina-Sanchez *et al.,* 2005). Plant height, which is a result of stem elongation, was significantly decreased in gourd species exposed to salinity (Yetisir and Uygur, 2009). Inhibited leaf growth is among the earliest visible effects of salinity stress in grasses, which was attributed to decreased cell division and expansion in the leaf's growth zone (Ortega *et al.,* 2006; Taleisnik *et al.,* 2009; Bernstein *et al*., 2010). Root growth and dry matter accumulation have also been found to be very sensitive to salinity in cotton seedlings (Chachar *et al.,* 2008), as have the shoots of *Setaria verticulata* (Ben Ahmed *et al.,* 2008). There is also evidence of salinity-induced reductions in growth and dry weight accumulation of all plant parts (Bernstein, 2013), for instance, in maize (Blanco *et al.,* 2008) and beans (Gama *et al.,* 2007).

Maas and Hoffman (1977) assessed salt-tolerance of 60 different crops (i.e., field crops, forage crops, vegetables, fruits and ornamentals) based on experimental work in field plots under relatively uniform soil conditions and optimal irrigation management. They calculated the relative crop yield (Y_r, where the maximum yield under non-saline conditions is considered 100%) of these crops as a linear function of the electrical conductivity (EC) of the saturated soil paste extract in the root zone (EC_e) using Eq. [1]:

$$Yr = 100 - B\,(EC_e - A) \qquad [1]$$

where A (dS m^{-1}) is the EC threshold of the saturated soil paste extract in the root zone at which yield just begins to decline, and B is the yield decrease percent of the maximum yield per unit EC_e increase. Maas and Hoffman (1977) grouped the studied crops into the following four salt-tolerance levels: sensitive, moderately sensitive, moderately tolerant and tolerant. However, these estimations of salt-tolerance were obtained under steady-state conditions, uniform salt distribution with depth and time, uniform water distribution achieved by flood irrigation, and unrestricted water supply (high leaching rate), conditions that rarely exist in the field. In addition, distinct differences in tolerance levels of the crops were also found between cultivars (Munns and Tester 2008). Nevertheless, this classification can provide a general orientation. According to this tolerance-degree classification, most crop plants have been assessed as sensitive to EC_e values >4 dS m^{-1} (USDA-ARS, 2008), which is a common salt level in arid and semi-arid soils.

The spread of soil salinity in recent years and its impact on agricultural production have been the main driving force for hundreds of studies, as well as many comprehensive review articles on salinity published in the last decades (e.g., Flowers, 2004; Parida and Das, 2005; Yamaguchi and Blumwald, 2005; Liang *et al*., 2007; Tuteja, 2007; Munns and Tester, 2008; Ashraf *et al*., 2009). Many of these publications cover specific aspects related to salinity and plant interactions. Substantial effort has been invested in studying the development of salt-tolerant cultivars by screening, conventional breeding, and genetic engineering. However, most of those attempts have been rather unsuccessful due to the complexity of the salt-tolerance trait, both genetically and physiologically (Flowers, 2004; Yamaguchi and Blumwald, 2005). The prospects for genetic engineering are indeed promissing, as genetic transformation of transport proteins, compounds for oxidant scavenging and for the formation of compatible organic solutes, and transcription factors for gene regulation have led to a number of salt-tolerant lines. Nevertheless, the successful production of salt-tolerant cultivars by genetic transformation is limited when they are grown under commercial conditions (Ashraf *et al.,* 2008b, 2009). This highlights the importance of assessing the traditional approaches taken with the plant and its environment to alleviate salinity hazard and improve plant performance under salinity. The main objective of the present paper is to review, analyze and discuss the studies published in recent years, which have investigated these traditional actions.

II. ALLEVIATION OF SALINITY HAZARDS BY IMPROVING THE PLANT ENVIRONMENT

A. Removal of Salts from the Root Zone

1. Salt Leaching and Irrigation Management and Technology

The soil solution in irrigated fields is frequently more saline than the irrigation water because of evapotranspiration, which leaves the salts from the irrigation water in the soil, and the dissolution of soil minerals (Rhoades, 1974). One way to alleviate salinity hazards in crop production is to remove the salts from the root zone by leaching. Salt leaching requires adequate irrigation management, which is based on adding sufficient amounts of water beyond the water requirement for meeting evapotranspiration demands, in order to leach the excess salt from the root zone (Russo *et al*., 2009). It follows that the higher the salt concentration in the irrigation water, the greater the amount of water that must be passed through the soil to keep the salt concentration in the root zone at or below a critical level. This approach to overcoming salinity has been intensively studied for many years. One of the earliest reports on this issue can be found in a handbook published by the U.S. Salinity Laboratory Staff (U.S.

Salinity Laboratory Staff, 1954), which was further discussed by Rhoades (1974). Since these publications, many other studies and reviews have been published on this subject (e.g., Hoffman and van Genuchten, 1983; Ayers and Wescot, 1985; Shalhevet, 1994; Hanson *et al*., 2006; Corwin *et al.,* 2007; Russo *et al*., 2009; Letey *et al.,* 2011).

Wheat yield and its components decreased significantly when the EC of the irrigation water increases from 2 to 12 dS m^{-1} (Mostafazadeh-Fard *et al*., 2009). However, under salt-leaching conditions, this decrease was more moderate. In a trial with bell peppers grown in lysimeters in a protected environment and irrigated with water at EC levels between 0.5 and 3.5 dS m^{-1}, it was found that the higher the salinity level of the irrigation water, the higher the benefits from the leaching process (Ben-Gal *et al*., 2008). These authors claimed, however, that under the experimental conditions, the extent of leaching needed to maximize yield maybe unsustainable. Barnard *et al*. (2010) studied the optimal amounts of water required to efficiently leach excess salts from the root zone of maize irrigated with water of 7.5 dS m^{-1} in a lysimeter experiment. They found that excess amounts of irrigation water, equivalent to 20% and 30% of the pore volume of the studied sandy and loam soils, respectively, were needed to efficiently remove 70% of the excess salts from the root zone. However, the salinity of the solution in the root zone of the studied soils approached the EC of the irrigation water only after leaching with a volume comparable to 90% of the pore volume of the irrigated soils, a volume that was not economically feasible (Barnard *et al*., 2010).

The leaching fraction (*LF*) is the actual fraction of the applied water that passes through and leaves the root zone. Leaching requirement (*LR*), however, is defined as the minimum fraction of the irrigation water that must be leached through the root zone to control soil salinity at a specific level. In practice, the *LR* could be defined as the minimum *LF* required to achieve the maximum yield of a particular crop under irrigation with a specific water quality (Letey *et al*., 2011). Under a steady rate of water flow, with no removal of salt by the crop, uniform areal application of irrigation water, and no precipitation of soluble salts, the *LR* can be calculated using Eq. [2] (U.S. Salinity Laboratory Staff, 1954):

$$LR = \frac{V_d}{V_i} = \frac{EC_i}{EC_{d\,\max}} \qquad [2]$$

where, V_d and V_i are the volumes (in mm) of water drained from the root zone and infiltrated irrigation water, respectively, EC_i is the *EC* (dS m^{-1}) of the irrigation water, and $EC_{d\,\max}$ (dS m^{-1}) is the maximum electrolyte concentration permissible in the soil solution for a certain crop. For example, $EC_{d\,\max}$ values are 4 dS m^{-1} for sensitive crops, 8 dS m^{-1} for tolerant crops such as beets, alfalfa and cotton, and 12 dS m^{-1} for very tolerant crops, such as barley (U.S. Salinity Laboratory Staff, 1954). For the calculation of *LR*, the $EC_{d\,\max}$ for various crops can be obtained from Maas and Hoffman (1977). For the $EC_{d\,\max}$ values, they suggested using the average EC values of the saturated soil paste extract of the root zone that resulted in 50% yield reduction of forage and vegetable crops and 10% reduction of fruit crops. Two main assumptions were made in this calculation of *LR* values: (i) the crop responds to the average root zone salinity, and (ii) the soil EC at field capacity is about twice that of a saturated soil paste extract (Corwin *et al.,* 2007). It should be emphasized that the leaching technique could be applied only under adequate drainage conditions, to allow leaching of the concentrated salt solution from the root zone. Under inadequate drainage conditions, the water table might rise in response to the excess water, potentially resulting in increased salinity in the root zone, and a possible decrease in crop yield (Ben-Hur *et al*., 2001).

The effects of *LF* on yield of citrus that was irrigated for 9 years by under-tree microsprinklers with irrigation water at four EC values ranging from 0.44 (control) to 2.50 dS m^{-1}, and *LF* values of 0.24 in the control treatment and 0.51 in the other salinity irrigation treatments were studied by Prior *et al*. (2007). An *LF* of 0.51 resulted in low or moderate salinity levels in the root zone throughout the experimental period, and in only a very few cases, this salinity exceeded 3 dS m^{-1}, even in the highest salinity irrigation treatment. The content of Na and Cl in the citrus leaves increased mainly with the highest salinity treatment, which decreased the yield by 17% and annual trunk diameter growth by 59% as compared to the control treatment.

A field trial was conducted on avocado trees, which are known to be extremely sensitive to salinity, in which three quantities of irrigation water (at an EC of 0.7 dS m^{-1})—90%, 110%, and 130% of estimated crop transpiration—were applied at three irrigation frequencies (one, three, and seven times a week) (Oster *et al*., 2007). Increasing amounts of irrigation water increased avocado yield in all irrigation treatments when the maximum salinity level in the saturated soil paste extracts in the root zone was equal to or less than 4 dS m^{-1}. Oster *et al*. (2007) concluded that the differences in the amounts of irrigation water have little effect on the EC in the root zone, but increase water availability to the crop before the soil salinity reaches approximately 4 dS m^{-1}, at which point water uptake is restricted. This was probably the reason for the higher yield with the larger quantities of irrigation water.

Several models have been proposed to calculate the *LR* for specific crops, irrigation water qualities, and environmental conditions. For instance, the SALTMED model of irrigation management was used to determine proper irrigation management for tomatoes grown in salt-prone soil (Flowers *et al*., 2005), and was further developed for sugarcane under semi-arid conditions in southwest Iran (Golabi *et al*., 2009). This model incorporated evapotranspiration, plant water uptake, solute transport, crop yield and biomass production, and was calibrated in a field trial over the course of two years, then verified in the third year. Golabi *et al*. (2009) found that the SALTMED model could be used successfully as a tool to determine the *LR* for sugarcane under saline and semi-arid conditions. After validating the SALTMED

model in an irrigation experiment with saline water of 8 dS m^{-1}, good-quality water (1.24 dS m^{-1}), and alternations between the two water types, Gawad *et al*. (2005) found it to be a good tool for determining proper irrigation and drainage management for tomato. In their review, Hanson *et al.* (2006) showed a linear relationship between EC of the soil solution and irrigation water at *LF* values between 0.05 and 0.50 for various crops, and the dependence of this relationship on irrigation methods and frequencies. These authors published a guideline for *LR* calculation for various crops based on salinity of the irrigation water and the crop's salt sensitivity (Hanson *et al.*, 2006). It should be stressed, however, that this guideline was based, in general, on steady-state water flow, disregarding salt precipitation and preferential flow, and on the assumption that salt concentration in the soil solution at any point in the root zone is constant with time (Corwin *et al.,* 2007; Letey and Feng, 2007).

More recently, new models have been suggested for calculating *LR* that take into account the soil/water interactions as dynamic processes (e.g., Corwin *et al.,* 2007; Letey and Feng, 2007; Isidoro and Grattan, 2011). Letey and Feng (2007) calculated the ratio between the quantities of applied waters of various qualities and the potential evapotranspiration that produce a specific relative yield of corn using a dynamic model, and compared it to two steady-state models, the Crop Water Production Function (CWPF) model (Letey *et al*., 1985) and the Enviro-Gro model (Feng *et al*., 2003). Letey and Feng (2007) found that the *LR* values predicted by the dynamic model were significantly lower than those calculated by the steady-state models. Letey *et al*. (2011) indicated that the steady-state models predict, in general, higher negative effects of irrigation with saline water on crop production than the dynamic models, due to the following: (i) In the steady-state approach, the plant response is to the average salinity of the entire root zone, when in fact, the plant roots extract water mostly from the upper soil layer, where salt concentration has less effect on *LF*. (ii) The steady-state approach considers the salt concentration in the soil solution to be a constant value throughout the season. However, it is well known that the salt concentration changes continuously in the root zone; it increases when water is taken up by the plants, it decreases sharply after irrigation, and its concentration in the upper soil layer becomes close to that of the irrigation water. (iii) It is generally assumed that the EC of the water surrounding the roots is about twice that of the saturated soil paste extract, but in practice, in most soils, the EC of the water surrounding the roots is lower. Corwin *et al.* (2007) compared *LR* values estimated by the steady-state WATSUIT model using the water-production function proposed by Letey *et al*. (1985) or by dynamic models, such as TETRANS and UNSATCHEM. Under irrigation of croplands in Imperial Valley, California with water from the Colorado River (EC of 1.23 dS m^{-1}), they found *LR* values of 0.13 and 0.08, estimated by the steady-state and dynamic model, respectively. It can thus be concluded that switching the calculation approach from steady-state models to dynamic ones decreases the estimated *LR* values; this could lead to substantial water savings, and reduced chemical movement toward the groundwater.

In many regions, such as the Mediterranean, the climate is characterized by a long, hot, and dry season (summer) and a short rainy season (winter). Under these conditions, the salts accumulated in the soil profile during the irrigation season in the summer could be leached from the root zone by the winter rainfall (Ben-Hur *et al.*, 2001; Lado *et al.*, 2012). The effectiveness of this leaching is controlled by the water-holding capacity of the soil and the properties of the rainfall. For instance, the water-holding capacity of a 1 m layer of sandy soil is approximately 150 mm and of a clayey soil approximately 400 mm (Shalhevet, 1994). Thus, annual rainfall of 300 mm (an amount comparable to 2 pore volumes of the sandy soil) could leach most of the accumulated salt in the sandy soil, but only some of the salt in the clay soil (Shalhevet, 1994).

Another important factor that can control the salt-leaching efficiency of rainfall is the rainfall distribution throughout the year; for example, many rainstorms with small amounts of rain and long dry periods between them can show diminished salt-leaching efficiency. These factors are not considered by the steady-state models, but are considered by the dynamic models for *LR* estimation (Shalhevet, 1994). A simulation model (Isidoro and Grattan, 2011) showed that salt leaching from the root zone is more effective under concentrated rainfall during the winter season (pre-season leaching) than under rainfall distributed throughout the year (mid-season leaching). Using the MOPECO-Salt model, which was validated in an experiment with onion carried out in Albacete, Spain, Dominguez *et al*. (2011) showed that the pre-season leaching strategy reduces the amount of irrigation water required by 14%. Pre-season leaching was also shown to be preferable to mid-season leaching under shallow groundwater conditions (Forkutsa *et al*., 2009). Pre-season leaching reduced the irrigation amount needed for salt leaching, consequently preventing the development of secondary salinization.

Although high-quality water is recommended for salt leaching during the irrigation season, it can also be achieved with saline water (Ahmed *et al.,* 2007). It is generally accepted that increasing the quantity of irrigation water, in the case of saline water, may at least partially offset the negative effects of salinity (Russo *et al*., 2009). Under conditions of extreme water scarcity, determining the tradeoff between allocating water for leaching vs. crop production becomes critical. A non-linear optimization model to determine the impact of declining water quality on economic efficiency of irrigation was developed by Matthews *et al*. (2010). In that model, salinity of the soil solution, crop yield production, and leaching functions were used to indicate the interactions involved in water-allocation decisions. The model showed that under limited water availability in terms of time and location, it is more profitable to reduce the irrigated area, and allocate water for leaching (Matthews *et al*., 2010).

Another irrigation strategy to overcome salinity problems is switching the irrigation water from good-quality water to saline

water or vice versa during the growing season. Yadav *et al.* (2004) found that irrigation of some forage crops with drainage water at EC values ranging from 3.6 to 7.4 dS m^{-1} decreased the yields by 35 to 85% of those obtained under irrigation with good-quality (canal) water. However, irrigation with the canal water during crop's establishment, and then switching to irrigation with drainage water, led to significantly higher yields for all of the studied crops than irrigation with only the drainage water from the begining of the growing season (Yadav *et al.,* 2004). An additional approach to overcoming salinity problems is blending available waters of different qualities to achieve acceptable water quality for a given crop (Mostafazadeh-Fard *et al*., 2009). Wang *et al*. (2007) concluded, on the basis of 49 irrigation schemes (7 salinity concentrations and 7 irrigation schemes) for wheat and cotton, that if the irrigation water salinity is higher than 7.0 g L^{-1} only fresh water should be used, whereas if it is lower than 3.0 g L^{-1} this source can be used for irrigation; if the salt concentration lies somewhere between these values, the two sources should be mixed.

A considerable number of studies, mostly based on models, have been conducted to develop proper irrigation management to overcome salinity hazards (e.g., Feng *et al.,* 2003; Sepaskhah *et al*., 2006; Shani *et al*., 2007; Mandare *et al*., 2008). Feng *et al.* (2003) developed a model (ENVIRO-GRO) that estimated the relative yields of maize irrigated by water of various salinity levels (1.7 to 10.2 dS m^{-1}) and irrigation intervals. Verification of this model in a field experiment indicated (i) good agreement between the model's simulated runs and the field measurements for all salinity levels and irrigation intervals, and (ii) that the model considered the osmotic and matric stresses in the field under salinity conditions correctly. Sepaskhah *et al*. (2006) developed a model to determine the yields of sugarbeet, winter wheat and maize under various irrigation frequencies, salinity levels, and *LF* values. This model was calibrated and validated with data obtained from field experiments in a semi-arid region, and was found to be an efficient tool for determining proper irrigation management with water at different salinity levels.

A model named Soil, Water, Atmosphere, Plant (SWAP) simulated the effects of irrigation with different amounts of good-quality water from a canal (average EC of 0.5 dS m^{-1}) and saline groundwater with EC values fluctuating between 1.7 and 9.8 dS m^{-1} on soil salinity and yields of wheat grown from November until April and rice grown from June until October (Mandare *et al*., 2008). The model could be used as a guideline for improving irrigation management with saline water so as to maintain the soil salinity below a threshold level which maintains high crop yield. Steppuhn *et al*. (2005) studied the relationships between average root-zone salinity and wheat yield in a field experiment conducted in Canada's Salt Tolerance Testing Facility, and found that Eq. [3] best describes them:

$$Y_r = \frac{1}{1 + \left(\frac{C}{C_{50}}\right)^{\exp(sC_{50})}} \qquad [3]$$

where, Y_r is the relative yield of crop when the yield under nonsaline condition is defined as 1.0, C is the EC (dS m^{-1}) in saturated soil paste extract of the root zone, C_{50} defines C at $Y_r = 0.5$, and s is the absolute value of general decline in Y_r with salinity at and near C_{50}.

Crop production functions for wheat grown under saline conditions were obtained by pot experiments in the greenhouse in North Golestan Province, Iran (Kiani and Abbasi, 2009). The wheat was irrigated with four different amounts of water, ranging from 50% to 125% of the crop water requirement, and four levels of salinity ranging from 1.5 to 14.2 dS m^{-1} (Kiani and Abbasi, 2009). In this experiment, wheat yield responded more markedly to the reduction in matric potential than to that in osmotic potential, with dynamic functions best predicting wheat yield under the experimental conditions. An analytical model based on a more general mechanism and that integrates crop yield, anount of irrigation water, soil type, and salinity was developed by Shani *et al*. (2007). They claimed, for instance, that in the arid zone of the Arava region, Israel, where irrigation water salinity is around 3 dS m^{-1} and a drip system is used, the maximum potential yield of bell pepper at any *LF* value is 70% of its maximum potential yield under irrigation with fresh water.

Use of advanced irrigation technology is another important means of mitigating the salinity problem in agricultural fields. With surface and sprinkler irrigation systems, the applied water covers the entire soil surface of the cultivated field, and therefore salt leaching below the root zone occurs throughout the entire field. In contrast, with drip irrigation, only part of the field is wetted, and the salts are leached from the wet soil volume adjacent to the emitters, where nearly all of the roots are located. In this case, the salts accumulate at the periphery of the wet zone. Consequently, in drip irrigation, the plant roots exist mostly in the soil volume with relatively low salinity level, so salt leaching from the entire cultivated field during the irrigation season is not needed. However, prior to the following growing season, salt leaching below the root zone should be conducted in the entire field, due to the shift in the plants' location in the field every growing season. Several studies (e.g., Wan *et al*., 2007; Malash *et al*., 2008; Romic *et al*., 2008; Chen *et al*., 2009) have indicated the advantages of a drip irrigation system under saline conditions. In a field experiment with sunflowers irrigated with saline water (6.7 to 10.9 dS m^{-1}) using a drip system, Chen *et al*. (2009) found a yield decrease of 18% for every 1 dS m^{-1} increase in the irrigation water, when the soil matrix potential underneath the dripper was above −20 kPa. In another three-year field experiment conducted in the North China Plains with tomato irrigated with a drip system, irrigation with water at EC $\leq$ 4.9 dS m^{-1} had an insignificant effect on fruit yield (Wan *et al*., 2007).

In a field experiment conducted in Shibin El Kam, Egypt, Malash *et al*. (2008) compared growth parameters such as plant dry weight, leaf area index, water use efficiency (WUE), total yield, and fruit weight, of tomatoes that were irrigated with drip

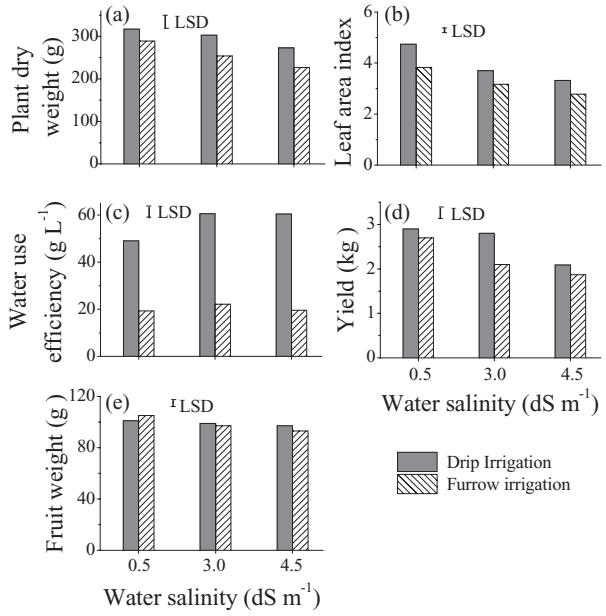

FIG. 1. Effects of irrigation systems (furrow and drip) on plant dry weight (a), leaf area index (b), water use efficiency (c), fruit yield per plant (d) and average fruit weight (e) of tomato plants irrigated with drainage water at salinity levels of 0.5, 3.0, and 4.5 dS m^{-1}. LSD = least significant difference between means at $\alpha = 0.05$ (following Malash *et al*., 2008).

or furrow irrigation systems and water of 0.5, 3.0 and 4.5 dS m^{-1}. The authors found that all of the measured crop parameters were higher under drip than furrow irrigation for all water qualities (Figure 1). In a field experiment conducted in Nereteva River Valley in South Croatia, Romic *et al*. (2008) compared the yields of watermelons irrigated by drip or sprinkler irrigation systems, when the salinity levels of the irrigation water were 1, 3, 5, or 7 dS m^{-1}. They found that irrigation with water of 3 dS m^{-1} causes mortality of the plants under sprinkler irrigation, whereas with drip irrigation, there was a significant reduction in fruit yield only at EC >3.0 dS m^{-1} (Figure 2).

Applying water and nutrients at a rate close to that of plant uptake by high-frequency or pulsed drip irrigation enhances the growth and production of irrigated plants (Silber *et al.*, 2003).

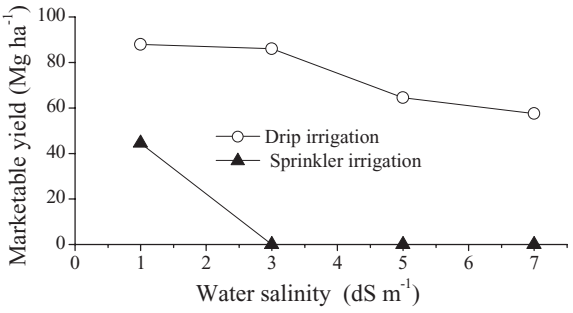

FIG. 2. Effects of irrigation systems (sprinkler and drip) on marketable yield of watermelon under different salinity levels of irrigation water (following Romic *et al*., 2008).

In contrast, Assouline *et al*. (2006) studied the effects of drip irrigation of bell pepper with saline water (4.2 dS m^{-1}) at daily or high frequency (pulsed irrigation), on the response of the soil-plant system. Salinity in the root zone and chloride content in the pepper leaves were higher under pulsed vs. daily irrigation, probably because the latter was more efficiant at removing salts from the root zone soil than the former.

2. *Primer and Companion Plants*

Another attractive approach for reducing salt content in the root zone is growing salt-tolerant plants either prior (primer plants) or simultaneously (companion plants) with agricultural crops. The idea behind this approach is that both primer and companion plants take up significant quantities of salt from soil solution, thereby reducing the salt content in the soil, and consequently establish a less saline environment in the root zone for the more sensitive agricultural crops (Colla *et al*., 2006; Nuttall *et al*., 2008). Nuttall *et al*. (2008) tested birdsfoot trefoil (*Lotus corniculatus*), canola, lucerne, safflower, sulla, and tall wheatgrass as primer plants prior to wheat planting, and found birdsfoot trefoil to be the best primer plant, resulting in the highest wheat yield. This indicated that the roots of the birdsfoot trefoil plant reduce the salinity levels in the root zone, which, in turn, allows proper growth of the wheat. Colla *et al*. (2006) studied the effect of *Salsola soda* as a companion plant to pepper growing in a greenhouse under saline conditions of 4.0 or 7.8 dS m^{-1} in the substrate solution. They found that under relatively low saline conditions (4.0 dS m^{-1}), the companion plant decreases the EC of the substrate solution by 45%, as well as the Na and Cl content in the pepper leaves. The total pepper biomass was significantly increased (by 22%), the fruit yield by 26%, and the mean fruit weight by 32% as compared to pepper grown without companion plants. However, under high saline conditions (7.8 dS m^{-1}), the *S. soda* companion plant had no effect on the yield of the tested pepper plant or on leaf Na or Cl contents. These results suggested that the companion plant approach is useful for relatively low soil EC levels (<4.0 dS m^{-1}). It should, however, be noted that when primer or companion plants are used in cultivated area, more water is needed per area for their demand.

3. *Soil Mulching and Water Treatments*

Covering the soil surface, mainly with plastic sheet or mulch, has been suggested to reduce the adverse effects of salinity, particularly in row crops (e.g., da Costa *et al*., 2008; Dong *et al*., 2008; Saeed and Ahmad, 2009; Bezborodov *et al*., 2010). The mulching is designed to reduce evaporation from the soil surface, and thus decreases salt accumulation in the upper soil layer. However, the interaction between salinity and mulching on plant performance is not always straightforward. The mulch may simply reduce the evaporation regardless of salinity, and thereby increase water availability, which, in turn, improves plant productivity. Only a few studies have attributed the effects of soil cover on plant production to its direct effect on

salinity. Mulching with plastic layers or wheat straw was tested in cotton, as a representative crop, by Dong *et al*. (2008) and Bezborodov *et al*. (2010). In those studies, the cover treatments increased lint yield by 25% (Dong *et al*., 2008) and by 800 kg ha^{-1} (Bezborodov *et al*., 2010) as compared to the non-mulched treatment. Dong *et al*. (2008, 2009) indicated that soil mulching under saline conditions decreases Na accumulation in the root and leaf tissues of cotton plants and inhibits lipid oxidation and malondialdehyde (MDA) activity, leading to an increase in net photosynthesis and biomass production of the cotton. Dong *et al*. (2009) showed additional improvement by the mulching technique when the cotton sowing was delayed to late spring, and the mulch was applied about 30 days prior to sowing. This treatment led to the additional contribution by increasing stand establishment, plant biomass, and lint yield as compared to conventional mulching technique, and was effective mainly under high-salinity conditions.

The effects of the amount of straw for mulching on yield and biomass production under saline conditions were studied for tomato by Saeed and Ahmad (2009), for amaranth by da Costa *et al*. (2008), and for maize by Pang *et al*. (2010). The latter authors compared the effects of various amounts of straw (4.5 to 30.0 Mg ha^{-1}) on maize irrigated with brackish water in which salt concentrations fluctuated between 3.0 and 5.0 g L^{-1} or with good quality water containing 1.27 g L^{-1} salts. In that study, the average salt concentration in the soil solution in the 0–20 and 20–40 cm soil layers was lower by 10.2% and 14.0%, respectively, for all mulch treatments as compared with the non-mulched treatment, and maize yield increased with increasing quantities of mulch. It was found, however, that except for a short period of time, there was no correlation between the amounts of mulch and salt concentration in the upper soil layer.

The effectiveness of different mulching types—gravel, rice straw and pine needles—in improving crop yield of Swiss chard and water saving under irrigation with saline water of 7.4 dS m^{-1} was investigated by Zhang *et al.* (2008). These types of mulch significantly reduced evapotranspiration and salt accumulation in the top soil layer, improved the biomass production of Swiss chard, and increased the WUE in the order: gravel > pine needles > rice straw > no mulch.

Treating the irrigation water prior to its application could also reduce the adverse effects of salinity. However, only a few studies have been explored the effects of this treatment on alleviation of salinity hazards. Aeration and magnetic treatments of the water prior to its application by subsurface drip irrigation were mainly tested. In tomato plants grown in saline and sodic clay soil and irrigated by subsurface drip irrigation, Bhattarai *et al*. (2006) found that enrichment of the irrigation water with 12% (v/v) oxygen increases shoot growth, fruit yield, mean fruit weight, fruit dry matter content, chlorophyll content, and WUE. In a pot experiment with soybean grown under saline conditions (2 to 20 dS m^{-1} in the saturated soil paste extract), Bhattarai and Midmore (2009) found that enrichment of the water with up to 12% oxygen prior to irrigation increases the relative water content in leaves, photosynthetic rate, biomass production, plant height, and stem diameter. Bhattarai and Midmore (2009) and Bhattarai *et al*. (2006) indicated that the beneficial effect of aeration of the irrigation water resulted from improved aeration conditions in the root zone of the saline and sodic clay soil which, in turn, enhanced plant performance.

A magnetic treatment of saline and recycled water prior to irrigation of celery, snow peas and peas slightly increases the yield and biomass production per unit water application, for celery and snow peas, as compared to irrigation with untreated water (Maheshwari and Grewal, 2009). However, it was not clear if these findings were connected to the salinity. Therefore, more studies on this issue are required for further verification and interpretation of this phenomenon.

B. Fertilizer Application to the Root Zone

Significant interactions between fertilization and salinity related to plant growth and production have been documented in many studies (e.g., Neves-Piestum and Bernstein, 2005; Cuin *et al.,* 2008; Edelstein *et al*., 2009; Jafari *et al.,* 2009; Sharif and Khan, 2009; Chen *et al.,* 2010; Fageira *et al*., 2011). These interactions for each specific nutrient and application to the root zone are reviewed and discussed in the following sections, while their foliar application is discussed in Section IV.F.

1. Potassium (K)

Potassium fertilizers are probably the most common fertilizers used to improve plant performance under saline conditions. The benefit of K fertilizer has been shown for various crops, including potato (Elkhatib *et al.,* 2004), lettuce (Ucar *et al.,* 2007), barley (Endris and Mohammed, 2007), strawberry (Khayyat *et al.,* 2009a, 2009b), pepper (Rubio *et al.,* 2009), endive (Tzortzakis, 2010), and sugarcane (Ashraf *et al.,* 2009, 2012). Figure 3 shows this effect for sugarcane.

The effect of K fertilizer has been assessed under different K concentrations (0 to 400 mg L^{-1}) and salinity levels (30 to ~ 130 mM) in the nutrient solution and under various environmental conditions. An increase in K concentration in the growing medium under saline conditions was shown to have the following beneficial effects on different crops: leaf length and surface diameter of lettuce were increased when K concentration in the growing medium ranged from 50 to 70 mg kg^{-1} (Ucar *et al.,* 2007); the harmful effects of NaCl on gas exchange and leaf area in strawberry were hampered (Khayyat *et al.,* 2009a, 2009b); potato tuber yield was increased by addition of K to saline irrigation water (Elkhatib *et al.,* 2004); number of tillers and kernels per spike and yield of barley were increased by addition of K to the saline irrigated water (Endris and Mohammed, 2007); the negative effects of salt on barley photosynthesis decreased when the K concentration in the growing medium increased (Degl'lnnocenti *et al.,* 2009). Other studies, however, found that in tomato (Yurtseven *et al*., 2005) and in some species of barley (Hafsi *et al*., 2007; Degl'lnnocenti *et al*., 2009), the negative

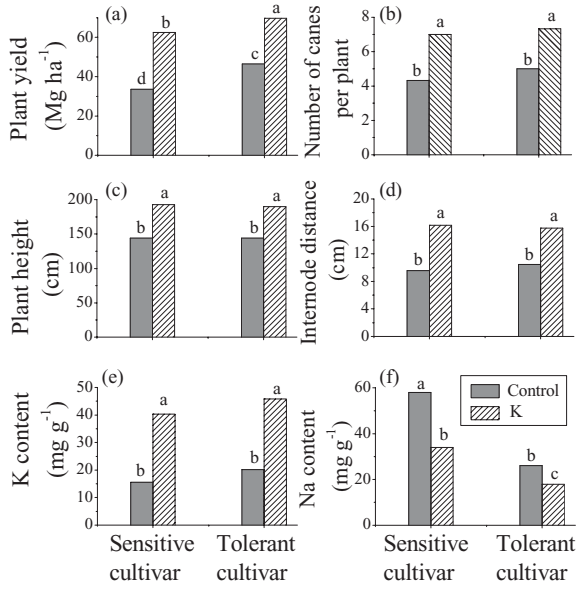

FIG. 3. Effects of adding 120 kg ha^{-1} K as K_2O (K) or no addition (control) on plant yield (a), number of canes per plant (b), plant height (c), internode distance (d), and leaf contents of K (e) and Na (f) in salt-sensitive and salt-tolerant sugarcane plants grown in saline soil with 10 to11.4 dS m^{-1} in the saturated soil paste extract. Columns with different letters in each subfigure indicate significant difference at $\alpha = 0.05$ according to Duncan's Multiple Range Test (following Ashraf *et al*., 2009).

effects of salinity on yield and plant growth are not prevented by an increase in K concentration in the growing medium.

Potassium may counteract the deleterious effects of Na by lowering Na uptake through root cells, which, in turn, improves the K/Na ratio in leaves, fruits or tuber cells of the fertilized plants (Hafsi *et al.,* 2007; Cuin *et al*., 2008; Degl'lnnocenti *et al.,* 2009; Ashraf *et al*., 2012). Ashraf *et al*. (2012), studying the response of sugarcane to NaCl (0, 100, 130 and 160 mM), suggested that the added K reduces the uptake of Na and its accumulation in plant tissues and consequently improves plant growth, yield and quality. Cuin *et al*. (2008) even suggested using the parameter of salinity-induced K flux in plants as a marker for breeding programs. In a later study, Cuin *et al.* (2010) indicated that two parameters, namely shoot-sap K concentration and chlorophyll content, should be used as tools for breeding salinity-tolerant plants.

Application of K as K_2SO_4 was shown to be preferable to its application as KCl. Ruan *et al*. (2007) found that application of K_2SO_4 increases the concentrations of amino acids in young shoots of tea plants, leading to improved yield quality. In contrast, chloride application reduced the yield of young shoots of tea plants and caused leaf damage. Fan et *al*. (2011) showed that 16 mM K as K_2SO_4 added to the nutrient solution containing 150 mM NaCl increased leaf growth and soluble sugars and proline concentration of tomato plants, resulting in their enhanced salt-adaptive capacity. In contrast, when 30 mM K was applied, soluble sugar concentration decreased, accompanied by a sharp increment in upper-leaf K concentration caused by the excessive K concentration in the nutrient solution.

2. *Calcium (Ca)*

Application of Ca fertilizers to plants under saline conditions could diminish the negative effects of salinity on plant growth, yield and fruit quality (e.g., Maeda et al 2005; Saleh *et al.,* 2005; Bolat *et al*., 2006; Jaleel *et al.,* 2007; Tuna *et al.,* 2007a; Jafari *et al.,* 2009; Rubio *et al.,* 2009; Sima *et al.,* 2009; Vaghela *et al*., 2010). Rubio *et al*. (2009) found that application of elevated Ca to tomato and pepper plants under saline conditions significantly reduces blossom end rot and enhances other fruit-quality parameters, leading to a significant increase in marketable fruit yield. Vaghela *et al*. (2010) found that under saline conditions, Ca application prevents the decrease in germination and growth of young seedling of *Salvadora persica* L., enhances N, P, and K uptake, and decreases Na accumulation in the leaves of the treated plants. Studies at the cellular level indicated that application of 2 mM Ca to nutrient solution containing 80 mM NaCl modulates the level of reactive oxygen species (ROS) in the expansion zone of leaf 4 in 14-day-old seedlings of maize, resulting in improved cellular expansion of the seedlings (Shoresh *et al*., 2011). Addition of 10 mM $CaCl_2$ to culture media containing 100 mM NaCl enhanced the exclusion of Na and resulted in improved growth of tobacco plants (Naeda *et al*., 2005). Jafari *et al.* (2009) found that combined application of Ca and K to sorghum plants grown under saline conditions partially eliminates the negative salt effects, and ameliorates plant growth and morphological traits.

It is interesting that an elevation in external Ca concentration improves plant growth and physiological activity, even at the very low external Ca/Na ratios of 1:10 to 1:150 (Tuna *et al.,* 2007a; Sima *et al.,* 2009). This indicates that Ca absorption by the plant is an active process, and not just a competition between ions. Several mechanisms have been suggested as responsible for the alleviation of salinity damage by Ca application in the growing media:

i. Supplemental Ca, mostly as $CaSO_4$, was found to specifically affect membrane permeability, leading to higher concentrations of Ca, K, and N, and a lower concentration of Na in the leaf cells (Naeda *et al*., 2005; Bolat *et al*., 2006; Tuna *et al.,* 2007a; Sima *et al.,* 2009).
ii. Elevated Ca concentration in the growth medium increased the accumulation of glycine betaine (GB) and proline in leaves of several plant species and plant callus, contributing to osmotic adjustment of the treated plants (Murugan and Sathish, 2005; Sima *et al.,* 2009).
iii. Increased Ca in the leaves (Jaleel *et al*., 2007) and growing leaf tissues (Shoresh *et al*., 2011) modulated the activity of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT), leading to increased protection of cells in the treated plants.

3. Nitrogen (N)

Studies on possible interactions between salinity and N fertilization have focused mainly on establishing optimal N application under saline conditions, rather than on its direct prevention of salinity hazards. Nutrient uptake in saline soils might be low due to high concentrations of cations and anions which might compete with the uptake of nutrient ions (Fageria *et al*., 2011). For example, Chen *et al.* (2010) found that N content in cotton plant tissues increases when N fertilization is increased under medium salinity levels (2.4 to 7.7 dS m^{-1}), but is not influenced at the high salinity level of 12.5 dS m^{-1}. Nadian *et al*. (2012) showed that the negative effect of salinity (4 to 8 dS m^{-1} in the irrigation water) on sugarcane yield and root growth is partially alleviated when the rate of N fertilizer is increased from 200 to 400 kg ha^{-1}. However, the higher rate of N fertilizer also improved K uptake and increased leaf proline content. In other study, Garg *et al*. (2006) found that increased N application, up to a rate of 60 kg ha^{-1}, to Indian mustard plants irrigated with saline water (2–10 dS m^{-1}) increased shoot concentrations of N, P and K and decreased Na concentration. The plants also displayed higher photosynthetic rates and more efficient N metabolism resulting in improved plant growth and seed yield. Similar findings were shown in a pot experiment with *Brassica juncea* grown in washed sand containing N in the range of 0–120 mg kg^{-1} and irrigated with saline water (90 mM NaCl) (Siddiqui *et al*., 2010). It was found in this experiment that the increase in N levels enhanced stomatal conductance and chlorophyll, malondialdehyde, and water content in the plant tissues. Similar results were found with chickpeas grown in a recycled nutrient solution, when increasing nitrate level up to 11 or 18 mM $NaNO_3$ at salinity levels of 12 or 36 mM NaCl increased the chickpeas yield (Tavori *et al*., 2004). Edelstein *et al.* (2009) studied the interaction between fertilization and salinity (1 to 6 dS m^{-1} in the irrigation water) on foliage biomass of vetiver (*Vetiveria zizanioides*) grown in pots in a heated greenhouse. They found a significant, negative linear regression ($Y = 1.6 - 0.08X$, $r^2 = 0.6$) between soluble NO_3^- and soluble Cl^- concentrations in the plant foliage (Figure 4), indicating that increasing NO_3 fertilization can decrease the uptake of Cl by the plant. This decrease was most likely the result of competition between the NO_3^- and Cl^- anions for their uptake by the plant roots (Edelstein *et al.,* 2009). On the other hand, Esmaili *et al.* (2008) recommended a lower level of N fertilizer (114 kg ha^{-1}) for sorghum grown under a salinity of 8 dS m^{-1} in the irrigation water, in contrast to 160 kg ha^{-1} which had resulted in maximal fresh and dry weight under non-saline conditions (0.6 dS m^{-1}). Barhoumi *et al.* (2010) found that in some forage grasses, a combination of high salinity and low N availability is the major limiting factor for plant growth and production. Thus, species with high and moderate salt-tolerance benefit from an increase in N supply at moderate salt levels, whereas salt-sensitive species did not.

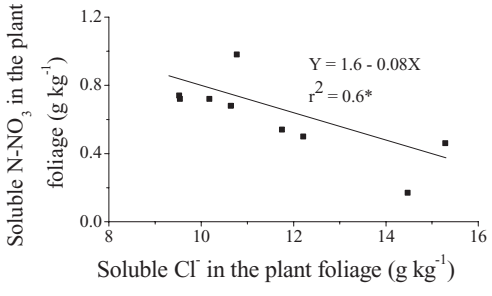

FIG. 4. Relationships between soluble N-NO_3 and Cl^- concentrations in vetiver foliage including regression line and equation (following Edelstein *et al*., 2009).

Some studies (e.g., Nathawat *et al.* 2007; Ashraf *et al.,* 2008c; Chen *et al*., 2010; Bybordi, 2011) have indicated that application of some chemical forms of N can reduce the adverse effects of salinity better than others. Nathawat *et al.* (2007) found that under saline conditions of 12 dS m^{-1} in the soil solution, application of N as NO_3^- to *Brassica juncea* cv. RH30 decreases the adverse effects of salinity on plant growth and net assimilation rates. Ashraf *et al.* (2008c) recommended using calcium-ammonium-nitrate (CAN) as an N fertilizer for sugarcane growth in saline soils. CAN application enhanced N, P, and K uptake and reduced Na accumulation in the leaves which, in turn, increased cane length and diameter, number of tillers, cane yield and sugar recovery (Ashraf *et al.,* 2008c). The effect of the ratio of ammonium to nitrate on alleviation of salinity damage of different tomato hybrids was studied by Ben-Oliel *et al*. (2004). They showed that application of 1 mM ammonium and 7 mM nitrate to constantly flowing nutrient solution containing 45 mM NaCl results in minimizing salinity effects on fruit yield.

The stage of irrigation at which N fertilizer should be applied under salinity conditions was studied by Hou *et al.* (2009). They found that application of N fertilizer to cotton grown under saline conditions (2.5–10.8 dS m^{-1} of the saturated soil paste extract) at the beginning of the irrigation cycle enhances N uptake, N-15 recovery and cotton seed yield. Application at later stages resulted in lower yield and higher potential losses of N from the root zone.

4. Phosphorus (P)

The possible ameliorative effects of P fertilization on salinity damage in plants have been less studied than those of other nutrients. Madueno-Molina *et al.* (2008) found that under high-saline conditions (100 mM NaCl in the growing medium), increasing P concentration in the nutrient solution from 4 to 8 meq L^{-1} enhances the growth of all organs of frijolillo (*Rhynchosia minima* L.). The increased P concentration augmented the osmotic adjustment of the frijolillo plants, in turn increasing their biomass production (Madueno-Molina *et al.*, 2008). Cimrin *et al*. (2010) found that in pepper plants grown under saline conditions (8 mM NaCl in the growing medium), application of P at levels between 50 and 150 mg kg^{-1} to the growing medium increases plant growth and yield. In a field trial with alfalfa irrigated with water containing 6.25 dS m^{-1} (El-Nakhlawy *et al*.,

2012), P fertilization reduced the adverse effect of salinity stress on alfalfa yield in 36 cuts performed over three years, whereas P fertilization had no beneficial effect under irrigation with saline water at 12.5 dS m^{-1}. An interaction between salinity and P application was also found for radish plants (de Oliveira *et al*., 2010). Increasing doses of applied P to 400 mg L^{-1} in irrigation water reduced the sensitivity of radish to salinity up to a level of 3.5 dS m^{-1}, resulting in increased leaf area and fresh and dry weight of roots. Since salinity reduces the transport of P in the plant (Martinez *et al*., 1996), improved P nutrition may overcome the salinity restrictive effects by increasing P availiability in the plant tissues.

5. Sulfur (S)

Sulfur nutrition has also been shown to reduce the adverse effects of salinity (Nazar *et al*., 2010). One of the functions of S in plants is the synthesis of cysteine, which is the final product of the sulfate reduction. Cysteine is a precursor or S donor for most organic S compounds, of which glutathione is probably the most important, as it is correlated with salinity tolerance and functions in the detoxification of ROS produced under salinity (Kocsy *et al.,* 2004; Nazar *et al*., 2010). Supplementary S fertilization of brassica and legume crops enhanced stress-defense mechanisms under abiotic stress conditions including salinity (Rausch and Wachter, 2005). Increased levels of S, up to 75 kg ha^{-1}, applied to field-grown wheat in a saline-sodic soil (EC 5.65 dS m^{-1}, pH 8.57, and sodium adsorption ratio 17.4 in saturated soil pate exracte) improved grain yield and yield component, the content of Ca and K in grains was significantly increased and that of Na was decreased, and the yield obtained with 75 kg ha^{-1} of S was 43% higher than the control without added S (Arshadullah *et al*., 2011).

6. Micronutrients

Fertilization with micronutrients could increase salt-tolerance in plants. For example, Zn reduced excess uptake of Na by pepper plants under saline conditions, probably by affecting the structural integrity and controlling the permeability of the root cell membrane (Aktas *et al.,* 2006). In this case, the Na content in the pepper shoot decreased, while K content increased. Symptoms of blossom end rot in pepper fruits were found when plants were grown in a recycling nutrient solution system at EC between 3.2 and 7.0 dS m^{-1}, and were associated with the production of apoplast ROS and increased NAD(P)H oxidase activity (Aktas *et al*., 2005; Bernstein *et al.,* 2005). Infiltration of Mn and Zn at concentrations of 5 mM into the fruit pericarp was shown to alleviate cellular symptoms caused by salinity (200 mM NaCl) and thus improve fruit quality. Wahid *et al*. (2009) found that in salt-sensitive varieties of sugarcane, the micronutrient content in the shoots and roots of plants decreases under saline conditions, and that this decline is highly correlated with a decrease in the plants' dry biomass. Therefore, Wahid *et al*. (2009) suggested that increasing micronutrient application in saline soils would enhance crop yield.

7. Biofertilizers and Manures

Biofertilizers, such as Nitrobein which contains species of the N-fixing bacteria *Azospirillum* and *Azotobacter*, and Phosphorine which contains the P-dissolving bacterium *Bacillus megatherium* var. *phosphaticum*, interact with salinity (e.g., Hasaneen *et al.*, 2009; Younis *et al.*, 2009b). Hasaneen *et al.* (2009) found that addition of Phosphorine to saline soils at levels between 4 and 10 dS m^{-1} induces a significant increase in all growth and reproductive parameters of lettuce, while addition of Nitrobein causes a slight decrease in these parameters. Younis *et al*. (2009b) studied the physiological mechanism responsible for this phenomenon, and found that photosystem II (PSII) activity and photosynthetic pigment and carbohydrate contents are increased by Phosphorine. These authors also found that application of Phosphorine and Nitrobein increases proline and glycine contents in lettuce leaves and that of several antioxidants in other plants exposed to salinity. However, no explanation was given for these phenomena, and therefore, further study of this matter is required.

Another way to add nutrients to cultivated soils is through the application of organic manures. However, some organic manure, such as poultry manure, could contain high concentrations of soluble salts, and their addition to the soil under saline conditions may aggravate the adverse effects of salinity on plant growth and yield. There are, however some organic manures that can be used as a source of nutrients without increasing the salt concentration in the soil solution. For example, Ahmed *et al.* (2010) found that adding farmyard manure to sand dune growth medium increases the dry matter production of wheat plants by 76% and 21% under salinity levels of 2.0 and 0.11 dS m^{-1}, respectively, in the growing media. These authors indicated that farmyard manure is a suitable nutrient source under saline conditions due to its relatively low content of soluble salts.

Application of composted municipal solid waste in a field with *Hordeum marinum* L. mitigates the adverse effects of irrigation with saline water of ~70 mM NaCl, and enhances the biomass production of the plants by 21% (Lakhdar *et al.,* 2008). This was a result of improvements in chlorophyll and Rubisco activity and protein contents in the plant tissues after addition of the compost. Application of humic acid was also found to dampen the deleterious effects of salt stress in pepper plants exposed to salinity, as it decreased the Na content in the shoots and roots and increased N, P, K, Ca, Mg, S, Mn and Cu contents in the shoots of the plants, consequently enhancing plant production (Cimrin *et al.,* 2010).

C. Application of Non-Nutritional Additives

A main element that is not essential for plant nutrition but is mostly applied to the root system to mitigate abiotic stresses, such as salinity, is silicon (Si). The mitigation of salinity hazard by Si has been outlined for a series of crops, such as rice, wheat, barley, cucumber, tomato and mesquite (Liang *et al*., 2007). The beneficial effects of Si on growth, chlorophyll content, membrane stability and leaf relative water content (RWC) in

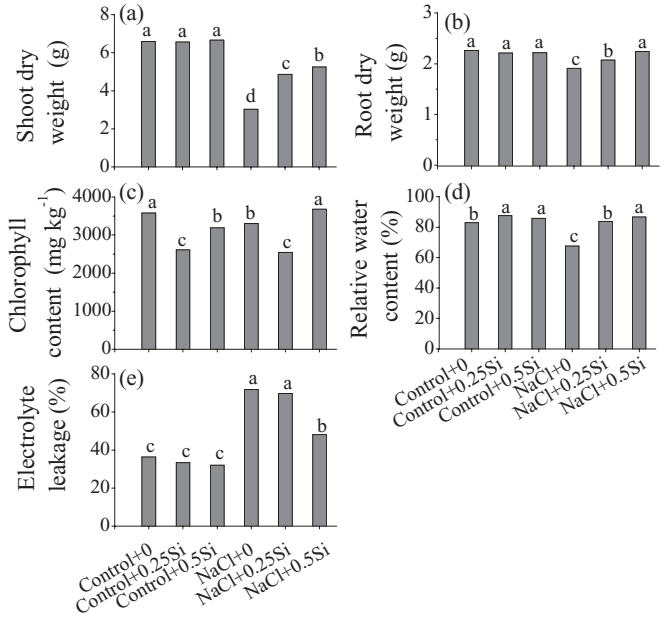

FIG. 5. Shoot (a) and root (b) dry weights, chlorophyll (c) and relative water (d) contents, and electrolyte leakage (e) in wheat cultivar Gediz-75 grown in low-salt nutrient solution (control) or in nutrient solution containing 100 mM NaCl (NaCl) and three Si applications: 0 (+0), 0.25 (+ 0.25Si) and 0.50 (+0.5Si) mM. Columns with different letters in each subfigure differ significantly at $\alpha = 0.05$ according to Duncan's Multiple Range Test (following Tuna *et al*., 2008a).

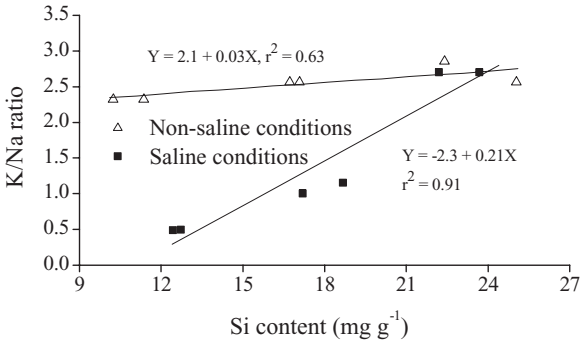

FIG. 6. Regression lines and equations between the K/Na ratios and Si contents in the foliage tissues of wheat irrigated with water containing 1.2 dS m^{-1} (non-saline conditions) and 11.9 dS m^{-1} (saline conditions) (following Tahir *et al*., 2011).

wheat plants (cultivar Gediz-75) grown under saline and non-saline conditions are demonstrated in Figure 5. Epstein (1994) was one of the first to document the benefit of Si in alleviating abiotic stresses, mainly in Gramineae species. Following that publication, a large number of studies (e.g., Liang *et al*., 2007; Savvas *et al*., 2007; Eraslan *et al*., 2008; Ashraf *et al*., 2009; Chai *et al*., 2010) were published and confirmed Epstein's (1994) findings. In most of those studies, the Si was applied as calcium silicate or as sodium metasilicate to the nutrient solutions at concentrations of <4 mM, and the beneficial effects of Si were studied under various salinity levels ranging from 35 to 150 mM NaCl in the nutrient solution or up to 12 dS m^{-1} in the soil solution.

Silicon uptake by the root system and its transport through the plant were found to be active processes in Gramineae plants, mainly rice and wheat (Liang *et al*., 2007), and passive processes in dicotyledonous plants (Liang *et al*., 2007), roses (Savvas *et al*., 2007), spinach (Eraslan *et al*., 2008), zucchini (Savvas *et al*., 2009), soybean (Lee *et al*., 2010), *Poa pratensis* (Chai *et al*., 2010), canola (Hashemi *et al*., 2010), and sugarcane (Ashraf *et al*., 2009). Tahir *et al*. (2006, 2010) claimed, however, that Si improves growth and grain production of wheat plants, even under non-saline conditions, suggesting that Si is not a true salinity-ameliorating substance. Conversely, in a later publication, Tahir *et al.* (2011) showed that adding 2 mM Si to a nutrient solution increases plant growth by 75% under saline conditions of 60 mM NaCl in the growing solution and by only 15% under non-saline conditions.

Although the mechanism underlying Si amelioration of plant growth under salinity is not fully understood, it has been claimed to be due to the restriction of uptake and/or transport of Na and Cl to young leaves, as was found in barley (Liang, 1999; Savvas *et al*., 2007, 2009; Ashraf *et al.,* 2009). This claim was further verified in wheat plants by Tuna *et al*. (2008a), Chai *et al*. (2010), and Tahir *et al*. (2010) who showed that Si reduces Na uptake by root systems and its transport to shoots. Moreover, Tahir *et al*. (2011) found that increasing Si application increases K content in the tissue of wheat plants grown under saline conditions of 11.9 dS m^{-1} in the nutrient solution, leading to a significant increase in the K/Na ratio in the plant tissues, while this ratio was less affected under non-saline conditions (Figure 6). Tuna *et al*. (2008a) indicated that for wheat grown under saline conditions and high Si concentration, an increase in Ca concentration in the nutrient solution might also contribute to wheat growth improvement. Liang *et al*. (2005) suggested that the increase in K^+ uptake and transport in plants under saline stress and Si application could be attributed to Si stimulation of the root plasma membrane H^+-ATPase. Another suggestion made by Liang *et al*. (2007) was that the application of Si decreases the permeability of the plasma membranes of leaf cells and improves the ultrastructure of chloroplasts under saline conditions. In other studies (Tuna *et al*., 2008a; Hashemi *et al*., 2010; Lee *et al*., 2010), it was found that addition of Si to wheat, canola and soybean plants grown under saline conditions increases leaf chlorophyll content. This might result in lower salinity-induced inhibition of photosynthesis. In fact, it was shown that under addition of Si, chloroplast activity enhances the photosynthetic rate, leading to improved plant growth (Savvas *et al*., 2009), whereas gas exchange in the leaves was hardly involved, because stomatal resistance was not affected by Si (Eraslan *et al*., 2008).

Another effect of Si on reduction of salinity harm is enhancement of antioxidant activity in plants. Eraslan *et al*. (2008) found that application of Si to spinach plants grown under salinity

conditions increases the activities of SOD and CAT and decreases the concentrations of hydrogen peroxide (H_2O_2) and malondialdehyde, as well as lipid peroxidation. An increase in the scavenging capacity of ROS was also shown when 2 mM Si was applied to canola plants grown under salinity of 150 mM NaCl in the nutrient solution (Hashemi *et al*., 2010). In most cases, the antioxidative activities decreased membrane damage and mediated their fluidity, thus improving membrane integrity and functionality (Zhu *et al*., 2004; Liang *et al*., 2005, 2007; Eraslan *et al*., 2008).

Changes in endogenous hormones, as a result of the addition of Si, could be another mechanism responsible for alleviation of the adverse effects of NaCl on plant growth and production. Lee *et al*. (2010) found that exposure of soybean plants to salinity decreases the level of gibberellins, which are associated with plant growth, while the levels of abscisic acid (ABA) and proline increased markedly in the plant tissues.

D. Treating the Aerial Environment

Treating the aerial environment of crop plants is most feasible in closed systems, such as glass or plastic greenhouses. The main environmental factors that can be controlled are: (i) aerial CO_2 concentrations, (ii) relative humidity, (iii) incoming radiation flux intensity, and (iv) rate of air exchange (ventilation), with only the first three factors being used to alleviate salinity's adverse effects.

1. Elevated CO_2 Concentrations

Elevated aerial CO_2 concentration in the plants' aboveground environment may enhance photosynthetic efficiency and lead to decreased leaf conductance due to stomatal closure, thus improving plant water status. A general analysis of the possible amelioration of salinity's adverse effects on plants by increasing aerial CO_2 concentrations in their environment was performed by Poorter and Perez-Soba (2001). These authors calculated the biomass enhancement ratio (BER), which was defined as the ratio of total plant biomass production under elevated aerial CO_2 concentration vs. normal (non-elevated) aerial CO_2 concentration. This calculation was conducted on the basis of available data in the literature on plants grown under a controlled aerial environment and salt-stress conditions. Although it was found in some experiments that the BER increases under high-salinity conditions, indicating that salinity stress is relieved by elevation of CO_2 concentration, Poorter and Perez-Soba (2001) stated that this amelioration is not significant. Other studies presented evidence of a more substantial effect of elevated CO_2 concentration on amelioration of salinity damage. Munns *et al*. (1999) found that an increase in aerial CO_2 concentration alleviates salinity's negative effects, but this effect was significant only at low salinity levels. On the other hand, Geissler *et al*. (2009a, 2009b) found that an increase in aerial CO_2 concentration significantly enhances photosynthesis and WUE of the halophytic plant *Aster tripdium*, even under saline levels close to that of seawater. This enhancement was attributed to mechanisms that reduce water loss, form thicker cell walls and cuticle, and increase chlorophyll and carotenoid content and ROS-detoxification activity. Although biomass production was hardly increased, proline synthesis was enhanced and improved plant water status and survival. An increase in aerial CO_2 also led to higher expression of the enzymes responsible for more active detoxification of ROS and for a β-ATPase, which is efficient in ion transport and homeostasis (Geissler *et al*., 2010).

An effect of elevated CO_2 concentration on antioxidant enzymes has also been found in glycophytes, such as various barley cultivars exposed to salinity levels of up to 240 mM NaCl (Perez-Lopez *et al*., 2009a). These barley cultivars showed better osmotic adjustment against salinity under elevated CO_2 concentration due to higher rates of photosynthesis, which increased the concentrations of sugars and other osmolytes in the plant tissues (Perez-Lopes *et al*., 2010). In that study, the osmotic adjustment was reflected by decreased dehydration due to stomatal closure, less negative plant water potential, improved turgor potential and higher WUE, as demonstrated in Figure 7. Salinity increased photochemical and biochemical limitations and thus increased non-photochemical quenching and reduced quantum

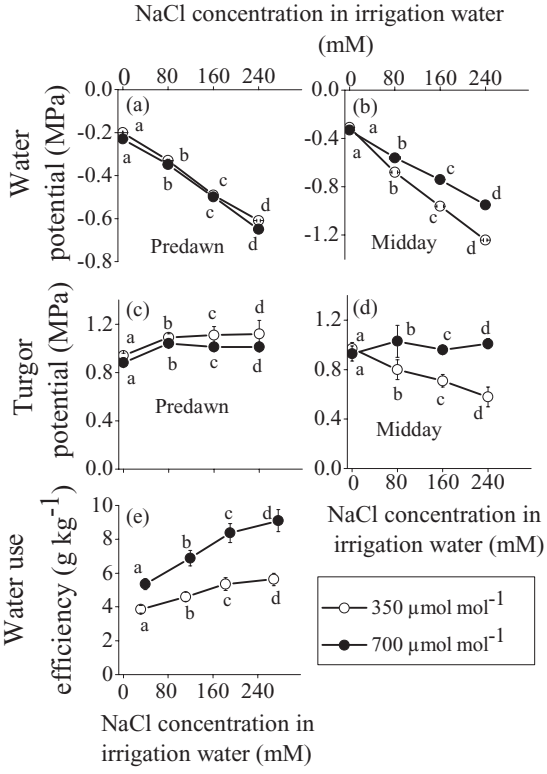

FIG. 7. Effect of NaCl concentration in the irrigation water on predawn (a) and midday (b) plant water potential, predawn (c) and midday (d) turgor potential, and water use efficiency (e) of barley plants (cv. Alpha) grown under aerial CO_2 concentrations of 350 and 700 μmol CO_2 per mol air. In each line and subfigure, symbols with the same letters are not significantly different at $\alpha = 0.05$ according to Duncan's Multiple Range Test (following Perez-Lopez *et al.*, 2009b).

yield of PSII. The higher CO_2 availability increased the electron sink capacity, which alleviated the salt-induced limitations on photosynthetic rate (Perez-Lopez *et al.*, 2012).

Salinity decreases the volumetric modulus of elasticity of leaf cell walls under normal aerial CO_2 concentration. Perez-Lopes *et al*. (2010) found, however, that elevation of CO_2 concentration limits this decrease, resulting in higher growth rates. Takagi *et al*. (2009) alleviated the negative salinity effects in tomato by increasing aerial CO_2 concentration: this augmented photosynthesis and assimilate transport, improved the plant water status through stomatal closure, and reduced oxidative stress, which, in turn, increased whole plant biomass production.

Some studies have indicated that elevated CO_2 concentration stimulates plant growth under saline conditions mainly via improvement of leaf water status rather than an increase in net photosynthesis. This was shown, for instance, in *Spartina densiflora*, a C4 halophyte exposed to salinity levels of up to 510 mM NaCl (Mateos-Naranjo *et al*., 2010a). In that study, net photosynthesis was not affected by elevation of CO_2 concentration from 380 to 700 mg L^{-1}, despite the fact that stomatal conductance decreased at 700 mg L^{-1} CO_2 because phosphoenolpyruvate carboxylase activity was enhanced. Mateos-Naranjo *et al*. (2010b) found that elevated aerial CO_2 concentrations under saline conditions also have a marked effect on photochemical activities (PSII), synthesis of photosynthetic pigments, and ratio of fluorescence to maximal fluorescence; all of these parameters increased under saline conditions when the aerial CO_2 was elevated from 380 to 700 mg L^{-1}.

Studies on the interactive effects of salinity and elevated aerial CO_2 concentration on trees are scarce. Melgar *et al*. (2008) showed that elevating CO_2 concentrations up to 700 mg L^{-1} increases net CO_2 photosynthesis and shoot growth of young olive trees, but this phenomenon disappeared under a salinity of 100 mM NaCl in the irrigation water. In this case, accumulation of Na and Cl in leaves and roots of salt-sensitive olive cultivars declined at elevated CO_2 concentrations, but not in salt-tolerant ones.

2. *Air Relative Humidity and Temperature*

Increasing the humidity in the greenhouse, which reduces the rate of transpiration, could mitigate the adverse effects of salinity on growth and crop production due to a reduction of the salt uptake by the plant. Biomass production of a relatively salt-sensitive tomato cultivar grown in 80 mM NaCl in nutrient solution declined much less at 70% than at 30% relative humidity (An *et al*., 2005). This ameliorative effect was attributed to increases in stomatal conductance, photosynthetic rate and leaf area, and a decrease in Cl accumulation in the leaves. In a study with several melon cultivars that were subjected to the same treatments as in An *et al*. (2005), An *et al*. (2002) found that: (i) Cl and Na contents in the leaves of salt-sensitive cultivars were significantly lower at 70% than at 30% relative humidity; (ii) the total biomass of the whole melon plant of the salt-sensitive cultivars increased with an increase in the relative humidity, regardless of salinity level; (iii) only root growth was enhanced in the salt-tolerant cultivars grown under saline conditions at increased relative humidity. In an experiment with tomato plants grown in a greenhouse and irrigated with saline water at an EC level of 9.5 dS m^{-1}, Li *et al*. (2001) found that fresh fruit yield increased by 8% in a treatment under low transpiration rate as compared to control plants (at high transpiration rates), but the dry matter content in fruits hardly responded to these treatments.

In a greenhouse experiment with tomato plants grown in nutrient solution containing 50 mM NaCl, Romero-Aranda *et al*. (2002) found that misting the greenhouse leads to a 1.0 to 1.5 kPa reduction in the vapor pressure deficit and a 5 to 7°C reduction in air temperature as compared to non-misted conditions. Consequently, the midday stomatal conductance and net CO_2 assimilation rates of the plants were three- to fourfold higher. The water uptake of the plants decreased by 15%, the leaf water potential became less negative, and the turgor, leaf area, dry matter production, and yield of the plants became higher under mist vs. non-mist conditions. All of these changes were, however, dependent on the availability of high-quality water for misting, because the use of saline water might do more harm than good to the crop.

Another environmental factor that can be controlled in the greenhouse is radiation intensity: shading can lower the air and plant canopy temperature. Farag *et al*. (2006) found that for cucumber plants grown under moderate saline conditions, shading the greenhouse increases growth and fruit yield. Misting the greenhouse increased cucumber yield more effectively under shading than under non-shaded conditions. Liopa-Tsakalidi (2008) found that reducing the air temperature from 18°C to 15°C markedly reduces germination inhibition of wild green vegetables grown under salinity of 40 to 80 mM NaCl in the soil solution. These salinity levels decreased the growth of roots and hypocotyls and delayed appearance of the first leaf in the wild green vegetables at 18°C. In contrast, at an air temperature of 15°C, only hypocotyl length decreased, and then only at the high salinity level of 80 mM NaCl (Liopa-Tsakalidi, 2008).

III. ALLEVIATION OF SALINITY HAZARDS USING BACTERIA AND MYCORRHIZAL FUNGI

A. Inoculation with Bacteria

Several studies have raised the possibility of increasing plants' salinity tolerance by inoculating the roots with salt-tolerant bacteria. These studies are based on evidence that ethylene synthesis is accelerated under salinity, which adversely affects root and whole plant growth (Saleem *et al*., 2007; Naeem *et al*., 2010). Jalill *et al*. (2009) found an increase in the amount of 1-aminocyclopropane-1-carboxylate (ACC), a precursor of ethylene biosynthesis, in plants under salinity stress, which led to an increase in ethylene production. Ethylene production can be reduced by application of ACC-deaminase, which metabolizes ACC into α-ketobutyrate and ammonia, thereby inhibiting ethylene synthesis (Saleem *et al*., 2007; Naeem *et al*., 2010).

Several plant-growth-promoting rhizobacteria (PGPR) of the genus *Pseudomonas* contain this enzyme, and when inoculated into plant roots may sustain plant growth under salinity (Egamberdieva and Kucharova, 2009; Jalill *et al*., 2009; Zahir *et al*., 2009; Naeem *et al*., 2010; Shukla *et al*., 2012). *Pseudomonas putida* and *P. fluorescens* alleviated salt stress in wheat, even at a saturated soil extract EC of 15 dS m^{-1}. The inoculated plants had higher K/Na ratios, relatively higher water and chlorophyll contents, and increased plant height, root length, plant biomass, and grain yield (Naeem *et al*., 2010). In a recent study, Shukla *et al*. (2012) compared six PGPR strains for their involvement in salt-stress tolerance of *Arachis hypogaea* grown hydroponically with 100 mM NaCl in the growing solution. Three bacterial strains—*Brachybacterium saurashtrense, Brevibacterium casei* and *Haererohalobacter*—resulted in best growth of *A. hypogaea* seedlings under salt stress. A higher K/Na ratio and higher Ca, P, and N contents were found in inoculated plants; shoot length and dry weight, root length and dry weight, and total biomass were all significantly higher in the inoculated plants. Inoculation of sweet pepper plants with *Azospirillum brasilense* and *Pantoea dispersa* prevented the decrease in leaf photosynthesis under 80 mM NaCl in the nutrient solution (del Amor *et al*., 2011). This was mainly due to higher stomatal conductance rather than an effect on biochemical limitations. The leaf Cl concentration in inoculated plants was reduced under salinity compared with control plants, and NO_3 concentration increased markedly. Higher K and Na ratios were found in inoculated plants as well.

Inoculation of artichoke plants grown in salinized nutrient solution (6.5 dS m^{-1}) and inoculated with *Bacillus subtilis* alleviated the adverse effects of salinity and increased productivity (Saleh *et al*., 2005). In pepper plants exposed to abiotic stress, inoculation with *Arthrobacter sp.* and *Bacillus* sp. upregulated the stressed inducible genes CaACCO and CaLTPI and reduced their down-regulation (Sziderics *et al*., 2007). Improved germination of canola seeds under salinity was also shown when the seeds were inoculated with strains of *Pseudomonas* producing ACC deaminase; seedling growth was thus enhanced (Jalill *et al*., 2009). Dimkpa *et al*. (2009) indicated that additional mechanisms may be responsible for the reduced salinity damage to plants, such as K uptake leading to a higher K^+/Na^+ ratio, a decrease in Na uptake, and diminished decrease in photosynthesis.

An increase in salinity tolerance of plants by inoculating the roots with salt-tolerant bacteria has been shown for several crops, such as pea, maize, groundnut, chickpea, faba bean, lettuce, pepper, tomato (Dimkpa *et al*., 2009; del Amor *et al*., 2011; Shukla *et al*., 2012)), barley (Omar *et al*., 2009) and radish (Yildirim *et al*., 2008b). However, the response of wheat appeared to be the most significant as both shoot and root growth were enhanced in plants exposed to 5% NaCl and inoculated with different *Pseudomonas* species (Egamberdieva and Kucharova, 2009). Moreover, plant height, grain and straw yield and 1000-grain weight were all increased (Zahir *et al*., 2009).

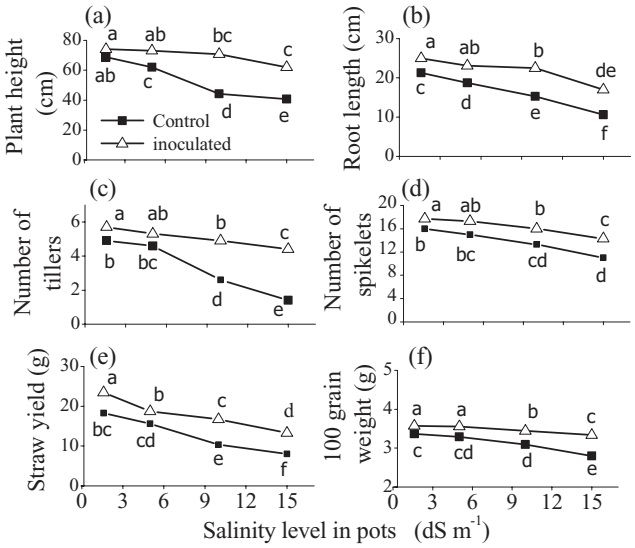

FIG. 8. Plant height (a), root length (b), number of tillers (c) and spikelets per plant (d), straw yield per plant (e), and 100 grain weight (f) of wheat as a function of salinity level in the saturated soil paste extract for two treatments: inoculation of plants with *Pseudomonas putida* containing ACC deaminase (inoculated) and non-inoculated plants (control). In each subfigure, symbols with different letters differ significantly at $\alpha = 0.05$ according to Duncan's Multiple Range Test (following Zahir *et al.,* 2009).

This can also be deduced from Figure 8, showing enhancement of all parameters of growth and yield production in wheat plants inoculated with *Pseudomonas putida* and exposed to different salinity levels up to 15 dS m^{-2} in pots. It is not clear whether the relationships between specific crop plants and specific bacterial species are essential, or whether any of those bacterial species would respond when inoculated on other plants. It should, however, be noted that the most effective rhizobacteria were *Pseudomonas putida* (Egamberdieva and Kucharova, 2009; Zahir *et al*., 2009) and *Pseudomonas fluorescens* (Jalill *et al*., 2009), isolated from the rhizosphere of wheat grown in salt-affected soils.

Mitigation of salt stress by rhizobacteria may also be achieved by incubating the seeds prior to sowing in a suspension of salt-tolerant bacteria. Pretreatment of radish seeds in a suspension of *Staphylococcus kloosi* or *Kokuria erythromyxa* significantly ameliorated the deleterious effects of salinity up to 80 mM NaCl (Yildirim *et al*., 2008a). Emergence percentage, shoot and root fresh and dry weights, leaf RWC, chlorophyll content and concentrations of nutrient elements in the plant were all increased, while electrolyte leakage was decreased.

Host plants may become tolerant to different levels of salinity depending on the extent of the inoculated rhizobacteria's salt-tolerance. Inoculation of a strain of *Azospirillum brasilense* isolated from hypersaline soil, which was able to survive up to 1800 mM NaCl, induced salinity tolerance in the host plant to high salinity levels. Omar *et al*. (2009) showed that the reduced growth and yield of barley plants exposed to 250 or 350 mM NaCl is markedly ameliorated by inoculation with *A. brasilense*

from a saline medium. The improved salinity tolerance of barley was due to increased pigment content and reduced activity of antioxidant enzymes.

Inoculation of mung bean seeds in peat-based inoculum containing *Rhizobium* and L-tryptophan improved growth and increased yield under saline conditions. The combined treatment of inoculation and application of L-tryptophan resulted in a more pronounced effect than applying them separately (Zahir *et al*., 2009).

B. Interaction of Plants with Mycorrhizal Fungi

A mycorrhiza is a symbiotic, mostly non-pathogenic association between a fungus and a vascular plant, in which the fungus colonizes the host plant roots. Mycorrhizas are divided into ectomycorrhizas (EMs), in which the hyphae of the fungi do not penetrate individual root cells, and endomycorrhizas, in which the hyphae penetrate the cells, also known as arbuscular mycorrhizas (AMs). The AM fungi are obligate fungi—they cannot grow in the absence of a host, whereas EM fungi can also grow as free-living organisms. Several mycorrhizal fungi of both groups have been shown to enhance salinity resistance in their host plants and may thus be used to improve plant growth and yield production under saline conditions.

1. *Ectomycorrhizas*

The alleviating effect of EMs on salt stress has been shown in herbaceous plants such as barley (Waller *et al*., 2005; Baltruschat *et al*., 2008), and in forest trees such as poplar, pine and spruce (Langenfeld-Heyser *et al*., 2007; Aguilar-Aguilar *et al*., 2009; Luo *et al*., 2009). The basidiomycete *Piriformospora indica* was found to be salt-tolerant and to induce tolerance to monocot and dicot plants (Langenfeld-Heyser *et al*., 2007). Studies conducted on barley as the host inoculated with this fungus showed enhanced activity of antioxidants such as dehydroascorbate reductase, and increased concentration of ascorbic acid (Waller *et al*., 2005). The activity of additional antioxidants such as glutathione reductase (GR), CAT, ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR) was also increased in salinity-exposed barley roots colonized by *Piriformospora indica* (Baltruschat *et al*., 2008). This resulted in attenuation of NaCl-induced lipid peroxidation, fatty acid desaturation and ultimately, increased growth of a salt-sensitive barley cultivar. Figure 9 shows the activation of these enzymes in plants inoculated with *P. indica* and exposed for two and four weeks to salinity. The most responsive antioxidants were DHAR, MDHAR and CAT.

The highly salt-tolerant fungus *Paxillus involutus* can attenuate detrimental salt effects on various host forest trees (Boise *et al*., 2006; Langenfeld-Heyser *et al*., 2007; Aguilar-Aguilar, 2009; Luo *et al*., 2009). Roots of salt-exposed poplar (*Populus canescens*) trees colonized by the fungus showed higher accumulation of ABA and salicylic acid (SA), known as stimulators of salinity tolerance, and a decrease in auxin and jasmonic acid as compared with non-EM-colonized' roots (Luo *et al*., 2009).

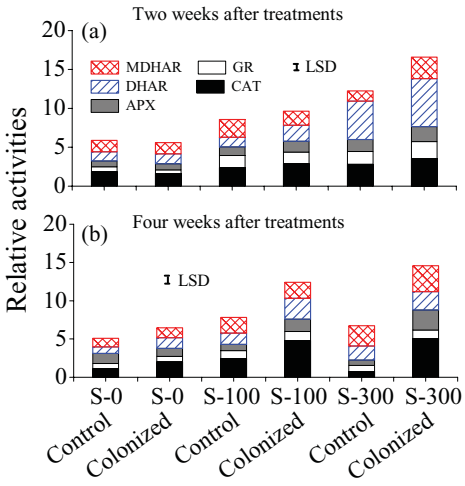

FIG. 9. Relative activities of catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX), dehydroascorbatereductase (DHAR) and monodehydroascorbatereductase (MDHAR) in roots of salt-sensitive barley cv. Ingrid irrigated with water containing ~0 (S-0), 100 (S-100), and 300 (S-300) mM NaCl after 2 or 4 weeks of root colonization by *Piriformosporaindica indica* (colonized) and non-colonized (control). The activity of non-colonized plants after 1 week and at S-0 salinity was defined as 1.0. LSD = least significant difference between means at $\alpha = 0.05$ (following Baltruschat *et al*., 2008) (color figure available online).

The K/Na ratio, carbohydrate accumulation and root cell volume were also increased in EM-colonized plants. In another study (Aguilar-Aguilar *et al*., 2009), colonization of the roots with EM also increased the concentration of osmolytes—proline, sugars and polyols, and stimulated the synthesis of antioxidant enzymes, which reduce ROS in those plants. Transcriptome analysis of salinity-exposed and EM-colonized poplar showed activation of genes related to abiotic stress response, probably leading to priming pathways that confer tolerance to salinity (Luo *et al*., 2009).

2. *Arbuscular Mycorrhizas*

The symbiotic association of crop plants with AM fungi provides nutrition to the host plant, as well as increasing water uptake, resistance to pathogens, production of hormones and adaptation to environmental stresses including salinity, as described by Garg and Chandel (2010). Similar enhancement of growth was found with AMs in salinized and non-salinized *Carthamus tinctorius* plants (Abbaspour, 2010), indicating that it does not specifically eliminate salinity damage. However, many other studies consider it an alleviator of salinity stress, as reviewed by Heikham *et al*. (2009). Here we will only present additional, as well as more recent information. Since AM fungi can be associated with many plant species (Hejiden *et al*., 1998), their use for the alleviation of salinity stress might be relevant for many crops. Crops which have exhibited such alleviation include wheat (Daei *et al*., 2009; Ibrahim *et al*., 2011; Talaat and Shawky, 2011), corn (Sheng *et al*., 2008, 2009), soybean (Sharifi *et al*., 2007), cotton (Tian *et al*., 2004), tomato

(Al-Karaki, 2006; Hajiboland *et al.,* 2010; Latef and He, 2011), lettuce and onion (Cantrell and Linderman, 2001), alexandrinum clover (Gharineh *et al*., 2009), subterranean clover (Asghari, 2008), citrus (Wu and Zou, 2009; Wu *et al*., 2010), grape rootstock (Belew *et al*., 2010) and several non-crop plants such as acacia (Giri *et al.,* 2007), *Carthamus tinctorius* (Abbaspour, 2010), *Trichosanthes dioica* (Mathur *et al*., 2010), *Tamarix, Phragmites, Sueda* and *Cirisium* (Wang *et al*., 2004). The AM fungi used for those plants were mostly different species of *Glomus*, but also some *Acaulospora, Entrosphora,* and *Archaeospora*, or mixtures of these.

In most studies, plants were inoculated with the AM fungus shortly before or shortly after exposure of the host plants to salinity. *Trichosanthes dioica* transplants were inoculated with *Glomus deserticola* and plants were then irrigated with saline water (EC of 2.6 dS m^{-1}) until harvest. This resulted in greater shoot and root dry matter and fresh fruit yield, which were enhanced much more in plants irrigated with saline water than in those irrigated with non-saline water (Mathur *et al*., 2010). The fungus *Glomus etunicatum* was pretreated with NaCl and then the inoculum was used for the host plant which had already been exposed to salinity. For instance, soybeans inoculated with the fungus and subjected to 100 mM NaCl showed higher fresh and dry weight, root proline content, and P, K and Zn concentrations as compared to non-salt pretreatment (Sharifi *et al*., 2007). Talaat and Shawky (2011) also found increased N, P, K, Ca, and Mg and decreased Na uptake in mycorrhiza-inoculated wheat plants exposed to salinity obtained by adding a mixture of NaCl, $CaCl_2$ and Mg SO_4 to the soil (up to an ECe of 9.38 dS m^{-1}). Soluble sugars, free amino acids, and proline were accumulated, and POX and CAT activities were higher than in non-inoculated plants. The detrimental effect of salinity was thus prevented and productivity was stimulated.

Maize plants grown under salinity and inoculated with AM fungi exhibited enhanced root development and activity as compared with non-mycorrhizal plants (Sheng *et al*., 2009). Root diameter and volume, and shoot and root mass were larger than in non-mycorrhizal plants (Sheng *et al*., 2009). It was suggested that the coarser root system and higher activity of the mycorrhizal maize roots assist in alleviating the effects of salt stress.

Inoculation of wheat plants with AM fungi mitigated the detrimental effects of salinity (6.09 dS m^{-1} and 10.63 dS m^{-1}) on electrolyte leakage, yield parameters and grain quality as compared to non-mycorrhized plants (Ibrahim *et al*., 2011). The highest root colonization with AM fungi was observed at the booting stage, whereas the lowest was reported at the tillering phase. Higher root and shoot dry weight was found in mycorrhizal subterranean clover plants exposed to salinity, with the most marked difference occurring at high salinity levels (Asghari, 2008). The beneficial effects of the mycorrhizal fungi were attributed to increased P uptake during early growth stages and increased K uptake during later stages, leading to an increased K/Na ratio in the roots. A similar response of dry weights to AM was found in another clover crop plant, *Trifolium alexandrinum*, grown under salinity (at EC of 10 dS m^{-1}), but it was still lower than under non-saline conditions (Gharineh *et al*., 2009). Plant dry weight was found to be decreased by different salts, but the sensitivity to NaCl was considerably higher than to all other salts, and the response to mycorrhiza was highest under NaCl salinity.

The response of tomato plants inoculated with the AM fungus *Glomus intraradices* and grown under salinity (EC of saturated soil extract of 5 or 10 dS m^{-1}) was studied by Hajiboland *et al*. (2010). They showed a different response of the antioxidant defense system in inoculated and non-inoculated plants. The mycorrhization also counteracted the salinity-induced reduction of P, Ca and K uptake, and increased the Ca/Na and K/Na ratios. Mycorrhization also improved net assimilation rates through both elevation of stomatal conductance and protection of PSII against salinity. The response of salinity-exposed plants to AM was also studied under field conditions. AM inoculation of wheat plants irrigated with saline water (nearly 14 dS m^{-1}) increased total dry weight, grain yield and nutrient uptake, and reduced the uptake of Na and Cl, as compared with untreated plants (Daei *et al*., 2009). It should be noted that different wheat cultivars responded differently to various AM fungi, and it may thus be important to select the optimal combination of fungus and host plant.

Fruit trees were also inoculated with mycorrhizae. Differences between cultivars' responses to mycorrhizal inoculation were shown in grape rootstocks, although all rootstocks showed a positive response to AM (Belew *et al*., 2010). Association of mycorrhizal fungi was also shown in citrus seedlings exposed to 100 mM NaCl (Wu and Zou, 2009; Wu *et al*., 2010), where the inoculated plants showed increased shoot and root dry weights, leaf number and area, plant height, stem diameter, root length, and surface area.

In addition to the studies on growth parameters and productivity, physiological parameters were also examined. Heikham *et al*. (2009) suggested a list of many physiological parameters which could be responsible for alleviation of the harmful effects of salinity on plants upon inoculation with AM. These were: (i) maintenance of a high K/Na ratio; (ii) improved acquisition of nutrients such as N, P, Mg and Ca; (iii) extended accumulation of proline, GB, polyamines, and carbohydrates; (iv) enhanced activation of antioxidant enzymes; (v) increased chlorophyll content and higher rates of photosynthesis; (vi) improved integrity and stability of cell membranes; (vii) higher hydraulic permeability and improved water status; (viii) increased number of nodules and nitrogen fixation by legumes; (ix) molecular changes, such as enhanced expression of the plasma membrane intrinsic protein (PIP) gene, expression of two Na^+/H^+ antiporters, and expression of genes encoding Δ1-pyrroline-5-carboxylase synthetase which catalyzes proline synthesis. Latef and He (2011) suggested that AM fungi play an important role in the protection of tomato plants against salinity (EC of 7.0 and 12.0 dS m^{-1}) by alleviating the salt-induced oxidative stress. In addition, the concentrations of P and K were higher and that of Na was lower

in AM-inoculated plants. As a result, leaf area, chlorophyll content, fruit fresh weight and fruit yield were increased.

Substantial evidence has been provided for improvement of ion composition in salinized plants inoculated with AM fungi. The main effect is probably a rise in K/Na ratio (Giri *et al*., 2007; Sharifi *et al*., 2007; Asghari, 2008; Wu and Zou, 2009; Wu *et al*., 2010; Talaat and Shawky, 2011). A rise in Ca/Na and Mg/Na ratios was also shown by Wu and Zou (2009) and Wu *et al*. (2010). Higher photosynthetic rates and improved plant water relations were found in citrus seedlings exposed to salinity and inoculated with AM fungi (Wu *et al*., 2010). A marked increase in the content of total free polyamines in mycorrhizal *Lotus glaber* plants grown under 200 mM NaCl as compared to non-mycorrhizal plants was outlined by Sannazzaro *et al*. (2007).

It is important to realize that despite the improved growth of AM-colonized plants grown under salinity, AM colonization can also be suppressed by salinity. In grape rootstocks, for instance, mycorrhizal colonization and spore number of *Glomus fasciculatum* were reduced under increased salinity levels (Belew *et al*., 2010). In citrus, salinity depressed *Glomus mosseae* colonization (Wu and Zou, 2009). In *Acacia fasciculatum*, colonization of *G. mosseae* was high up to a salinity level of 6.5 dS m^{-1}, but decreased at 9.5 dS m^{-1} (Giri *et al*., 2007).

IV. ALLEVIATION OF SALINITY HAZARDS BY TREATING THE PLANT

A. Seed and Young Seedlings Priming and Seed Size

Techniques of seed treatment prior to their sowing (seed priming) are aimed at the initial stage of the germination, but previous to the advanced metabolic and morphological changes in the seeds. Seed priming is expected to stimulate metabolic processes that normally occur during imbibition and are subsequently fixed by drying the seeds. Originally, seed priming was used to increase the rate and total germination of seeds with no connection to abiotic stress conditions, but it was then proposed for the alleviation of salinity hazards. Ashraf and Foolad (2005) reviewed the following priming techniques: osmopriming, halopriming, hydropriming, matric priming, thermopriming, priming with plant growth hormones, biopriming (coverage of the seeds with bacterial control agent) and drum priming (treating the seeds with less water than the amount needed for imbibition and germination, with no waste of the priming materials).

Salinity is known to adversely affect the seed germination process, leading to poor stand establishment and low final crop yield. It has been claimed that seed priming contributes to metabolic repair in seeds and the buildup of germination-enhancing metabolites, induces osmotic adjustment, and reduces the lag time of imbibitions (Ashraf and Foolad, 2005). However, the mechanisms that occur during seed priming are not well understood. Sivritepe *et al*. (2005) reported that priming of melon seeds in 18 dS m^{-1} NaCl solution for 3 days at 20°C decreases the negative effects of irrigation with saline water in the range of 4.5 to 18.0 dS m^{-1} on stomatal conductance, chlorophyll content and growth of the mature melon plants. In those plants, the contents of K and Ca in leaves increased, preventing the toxic effects of excess Na (Sivritepe *et al*., 2005). A positive effect of seed priming in 1% NaCl solution was also found for castor beans (Raghavaiah *et al*., 2006), and in 100 mM of $CaCl_2$ or KCl or NaCl solutions for spring wheat (Iqbal and Ashraf, 2007). These seed-priming processes increased grain yield and oil content in the castor beans, and net CO_2 assimilation, biomass production, and grain yield in the spring wheat grown under field conditions.

Plant hormones and growth regulators have been used intensively for increasing salt- tolerance of plants. Iqbal and Ashraf (2006) showed a consistent beneficial effect of priming of spring wheat seeds with 100–150 mg L^{-1} of kinetin or benzylaminopurine on growth and grain yield of plants grown in a field with NaCl salinity of 15 dS m^{-1}. Dolatabadian *et al*. (2009) found that soaking wheat seeds in a solution of saliciylic acid (SA) improves germination under salinity of <200 mM NaCl in the germination solution. Scavenging of ROS was more effective in treated plants, which limited membrane damage, enhanced the growth and germination rate of embryos, and increased cell division in young seedlings.

Additional plant hormones proposed for seed priming to alleviate the adverse effects of salinity are ABA and benzyladenine (BA). Gurmani *et al*. (2007) found that incubation of spring wheat seeds in solutions containing 10^{-5} M ABA or BA for 24 h prior to their sowing significantly increases the fresh and dry weights, number of grains per spike, total grain yield, and proline accumulation in the tissues of mature wheat plants grown under saline conditions of 100 mM NaCl in soil solution. In that study, it was also found that the wheat response to ABA and BA is generally similar, but that BA is more active than ABA in enhancing chlorophyll content, number of grains and grain yield. Gurmani *et al*. (2007) claimed that the positive effect of seed priming with ABA and BA under saline conditions is a result of limiting Na and Cl accumulation and increasing K accumulation in leaf tissues of the wheat plants. Al Hakimi and Hamada (2001) found that indoleacetic acid (IAA), gibberellic acid (GA), ascorbic acid, thiamine and sodium salicylate are effective in seed priming, and increase the growth and yield of the mature treated wheat plants irrigated with saline water at concentrations of 40 to 160 mM NaCl. Fariduddin *et al*. (2003) found that 28-homobrassinolide is effective in seed priming of mungbean. Three common polyamines, putrescine, spermidine and spermine, were also used for seed priming, and were shown to mitigate the salinity damage to shoot growth and grain yield of mature wheat grown in a field with 15 dS m^{-1} NaCl in the soil solution (Iqbal and Ashraf, 2005). The beneficial effect of the polyamines was cultivar-specific, but the effect of spermine was in most cases more pronounced than that of the other polyamines (Iqbal and Ashraf, 2006).

Manufactured plant-growth regulators were also used for seed priming to alleviate the harmful effects of salinity. Soaking seeds of *Vicia faba* in a solution with 10 to 30 mg L^{-1}

prohexadione-calcium prior to their sowing increased the shoot dry weight of plants grown in pots for 30 days and irrigated with saline water of about 2 to 3 g L^{-1} NaCl (Bekheta *et al*., 2009). The positive effect of prohexadione-calcium was probably due to the decrease in the endogenous content of GA and IAA in the treated plant tissues, which likely increased the proline, photosynthetic pigment and carbohydrate contents in the plant, and consequently increased the shoot dry weight (Bekheta *et al*., 2009). Bhadauria and Afria (2005) found that using the growth regulator Cycocel for seed priming also ameliorates the adverse effects of salinity in barley (Bhadauria and Afria, 2005).

Seed treatment with the soil fungi *Trichoderma harzianum* strain T22 sown in water-agar containing 50–150 mM NaCl resulted in faster and more uniform germination as compared to untreated seeds (Mastouri *et al*., 2010). It was claimed that this was due to accumulation of lipid peroxide in the seedlings.

Priming *Amaranthus lividus* (L.) seeds with the fungicide triadimefon was found effective at ameliorating negative salinity effects during the early developmental stages of the plants grown under saline conditions (Bhattacharjes, 2008). This seed priming reduced the oxidative damage to membrane systems of young plants and the losses of membrane proteins, and consequently restored membrane integrity and improved growth of the young seedlings. Stigmasterol, another fungicide, was claimed to have pleiotropic effects, since flax seed soaked in a solution containing 200 mg L^{-1} stigmaterol promoted growth, hormonal contents, phenylalanine ammonia lyase (PAL) activity, fiber quality, seed oil content and yield characteristics, and in general overcame stress provoked by NaCl (Hashem *et al*., 2011).

Increased salt tolerance could be also achieved by immersing young seedlings in solutions containing an inert osmoticum or salts. Parra *et al*. (2007) found that immersing young tomato seedlings in a solution containing polyethylene glycol at −0.75 MPa and 10 mM NaCl for three days prior to their planting increases shoot biomass and fruit yield, and decreases Na and Cl and increases K contents in leaves of mature plants that had been grown under saline conditions of 7.5 dS m^{-1} in the nutrient solution. It should be noted, however, that the optimal salt composition and concentration, as well as the duration of seedling soaking might differ for different species, and thus preliminary explorations are required to find the optimal conditions for seedling priming (Ashraf and Foolad, 2005). A somewhat similar approach involves acclimation of plants to salinity by gradually increasing the salt concentration in the growing media was indicated by Djanaguiraman *et al*. (2006). Rice plants were grown in 50 mM NaCl for seven days and then the concentration was raised to 100 mM; water potential was more negative, and leaf RWC, photosynthetic rate, stomatal conductance and chlororophyll content were higher as compared to plants which were directly exposed to 100 mM NaCl (Djanaguiraman *et al*., 2006).

Another possibility for overcoming salinity damage is to use a larger seed size for sowing. Steppuhn *et al*. (2009) studied the effects of seed size on alfalfa grown in tanks with sand that was flushed with hydroponic solutions containing nutrients and salts (mostly sulfates) at EC levels from 1.4 to 18 dS m^{-1}. They found that large seed size (2.16 g per 1000 seeds) improved germination and increased seedling height and their first-year forage production compared to small seeds (1.3 to 1.7 g per 1000 seeds). Gholami *et al*. (2009) found that bean seedlings which developed from large seeds had greater root and shoot lengths than those that developed from small seeds, when all of the seedlings were grown under osmotic pressures of -0.2 to -0.8 MPa. In contrast, Kaya and Day (2008) found that large seeds of sunflower produce vigorous germination and seedling growth under high-salinity conditions (10 to 20 dS m^{-1} in the nutrient solution) as compared to smaller seeds, but that the small seeds germinated and grew more rapidly and their seedlings developed more successfully under saline conditions as compared to the large seeds. In addition, Kaya *et al*. (2008) found a significant negative relationship between seed size and germination index or root and shoot length of chickpea plants that were grown under saline conditions. The above findings indicate that the use of large seed size as a technology to overcome salinity damage (Steppuhn *et al*., 2009; Gholami *et al*., 2009) requires further clarification and verification.

B. Grafting onto Tolerant Rootstocks

One environmentally friendly approach to avoiding or reducing salinity impairment in crop production is grafting salt-sensitive plants onto salt-tolerant rootstocks (e.g., Sykes, 1985; Colla *et al*., 2010; Edelstein *et al*., 2010; Yin *et al*., 2010). The technique of tree grafting has been known for about 2000 years, allowing adaptation to different environmental conditions, and providing improved scion growth and fruit yield (Webster, 1995; Storey and Walker, 1999). The importance of grafting in fruit trees to overcome salinity hazards has been shown in citrus (Sykes, 1985; Moya *et al*., 2003; Garcia-Sanchez and Syvertsen, 2006; Tavallali *et al*., 2008; Gimeno *et al*., 2009, 2010; Montoliu *et al*., 2009), wine and table grapes (Walker *et al*., 2004; Hepaksoy *et al*., 2006), pear and quince (Okubo *et al*., 2000; Matsumoto *et al.,* 2006; Musacchi *et al*., 2006), apple (Schreiner and Ludders, 1996; Molassiotis *et al*., 2006; Yin *et al*., 2010), loquat (Lopez-Gomez *et al*., 2007; Garcia-Legaz *et al*., 2008), prune (Massai *et al*., 2004), avocado (Mickelbart *et al*., 2007; Castro *et al*., 2009), mango (Schmutz and Ludders, 1998; Dubey *et al*., 2007) and pistachio (Tavallali *et al*., 2008), and in flowering shrubs, such as rose (Wahome *et al*., 2001). Grafting on salt-tolerant rootstocks under saline conditions brings about yield increases (Okubo *et al*., 2000; Walker *et al*., 2004; Garcia-Sanchez and Syvertsen, 2006) and improvements in product quality, as shown for Sultana and Cabernet Sauvignon grapes (Walker *et al*., 2004; Hepaskoy *et al*., 2006), enhancement of plant vigor and leaf growth of the scion (Lopez-Gomez *et al*., 2007; Gimeno *et al*., 2009), reduction in leaf necrosis as shown in 'Hass' avocado (Mickelbart *et al*., 2007), and diminution of Cl content in leaves as shown in roses (Wahome *et al*., 2001).

A major function of the tolerant rootstocks is preventing the accumulation of toxic ions in the leaves, thus allowing proper physiological activities. Native Mediterranean *Pyrus* rootstocks exhibited higher photosynthetic rates than Asian species because the former rootstock accumulated less Na and Cl in the leaves (Matsumoto *et al*., 2006). Similarly, grafting avocado cv. Hass scions on Nabal rootstocks limited Cl content in the leaves, resulting in high carbon-assimilation rates (Castro *et al*., 2009). This was also documented in peach plants grafted onto salt-tolerant *Prunus* rootstock, where full recovery of photosynthetic performance was detected after salinity stress (Massai *et al*., 2004). Under saline conditions, leaves of Golden Delicious apple trees grafted on M9 rootstock displayed greater stomatal conductance, transpiration rates, and accumulation of organic osmolytes than trees grafted on M26 rootstock (Schreiner and Ludders, 1996). Irrigation with saline water (50 mM NaCl) had insignificant effects on gas exchange, stomatal conductance, or net CO_2-fixation in leaves of loquat plants grafted on anger rootstock, whereas these parameters were significantly affected in self-grafted trees (Garcia-Legaz *et al*., 2008). Tolerant rootstocks of grape limited Cl content in the petiole, leaf lamina and juice (Walker *et al*., 2004). In a later study, Walker *et al*. (2010) showed that grafting also improves the quality of juice and wine. For example, Shiraz on its own rootstocks, K51–40, and 1202C rootstoks, accumulated unacceptable levels of Cl in the juice and wine when the salinity of the irrigation water was 1.8 to 3.3 dS m^{-1}. In contrast, the rootstocks Schwarzmann and 140 Ruggeri were best with Chardonnay and Shiraz, respectively. Pear roots adopted an ion-exclusion strategy to avoid accumulation of Na and Cl, whereas pear trees grafted on quince adopted a strategy of storage of most of the absorbed Na in the root system (Musacchi *et al*., 2006). Similar storage of the absorbed Na was documented in pistachio rootstocks, showing that the Ghazvini rootstock copes better with salinity than other rootstocks due to inhibited transport of Na from the roots to the leaves.

Salinity tolerance in citrus is mainly a result of lower root-to-shoot transport capacity, as found in Cleopatra mandarin with decreased Cl accumulation in the leaves as a result of decreased Cl loading into the xylem, leading to increased tolerance to salinity (Brumos *et al*., 2010). Direct measurements of Cl concentration in the xylem were conducted by Raveh and Levy (2005), and could be used as an efficient approach for analyzing Cl loading into the xylem with no need to monitor changes in leaf Cl content. Another interesting approach to increasing salinity tolerance in trees is the use of tetraploid genotypes as rootstocks, when the diploid genotypes of the same plant are not tolerant to salinity. For instance, Saleh *et al*. (2008) showed that the tetraploid genotypes of Cleopatra were less affected by mild salinity conditions than their diploid genotypes.

Since in fruit trees the responses of fruit yield and quality to salinity can be detected only after several years, it is desirable to evaluate the tolerance of rootstocks or grafted trees at an early stage. Early evaluation can be achieved by studying the response of rootstocks to salinity at the seedling stage, or as explants, rather than in mature trees. The relative tolerance of 15 types of apple rootstock exposed to 200 mM NaCl in the nutrient solution was successfully determined based on growth parameters such as leaf number and plant height, activities of antioxidant enzymes, and accumulation of organic osmotica in plant tissues (Yin *et al*., 2010). Dubey *et al*. (2007) found a significant negative correlation between dry matter production of shoot and roots and Na content in leaves of two rootstocks of mango that are sensitive to salinity. They concluded that the analysis of Na content in leaves could serve as an indicator of salinity sensitivity. Molassiotis *et al*. (2006) indicated that Na accumulation in leaves of rootstock explants is the first candidate for antioxidant activity and anatomical responses of the rootstock to salinity. Montoliu *et al*. (2009) successfully determined salt-tolerance of different citrus rootstocks in vitro by using nodal segments of these plants. In grapes (cv. Sultana), Walker *et al*. (2004) found that a combination of innate high vigor and moderate or high Cl and Na exclusion by the rootstocks was a good indicator of salt-tolerant plants.

As grafting of vegetable crops becomes more common to prevent damage caused by soil-borne pests and pathogens (Oda, 2002), such grafting is also being recommended to ameliorate injury due to salinity (e.g., Santa-Cruz *et al*., 2002; Rivero *et al*., 2003; Ruiz *et al*., 2006; Wei *et al*., 2007; Uygur and Yetisir 2009; Colla *et al*., 2010; Edelstein *et al*., 2010). Comprehensive review papers have been recently published by Colla *et al*. (2010) and Edelstein *et al*. (2011) showing that grafting of vegetable plants limits the reduction in total yield, biomass production, leaf area, and plant height of vegetable plants exposed to different levels of salinity. For instance, a recent study by Liu *et al.* (2012) showed that the reduction in growth of cucumber plants grown in 0.5 Hoagland solution containing 90 mM NaCl is less in grafted plants than in non-grafted ones, mainly due to enhanced net photosynthetic rates, stomatal conductance and quantum yield of PSII in the grafted plants. Colla *et al*. (2010) stressed the importance of the scion in the growth of grafted tomato and cucumber plants, and that salt-tolerance conferred by the rootstock is also dependent on the salt-tolerance of the shoot. However, other studies (Blom-Zanstra *et al*., 1998; Shaterian *et al.,* 2005; Edelstein *et al.,* 2007) emphasized the major importance of rootstock characteristics in determining salt and boron (B) tolerance of grafted plants. Edelstein *et al*. (2010, 2011) studied the effects of grafting on accumulation of Na and B, respectively, in shoots of grafted and non-grafted plants in a greenhouse experiment. In those studies, six combinations of melon (cv. Arava) and pumpkin (cv. TZ-148)—non-grafted, self-grafted, melons grafted on pumpkins and pumpkins grafted on melon—were used. The relative shoot and root yields in all of the non-grafted and grafted plants decreased as B concentration in the irrigation water increased (Figure 10). The shoot dry weights of the grafted plants at a B concentration of 10 mg L^{-1} (Figure 10) and under irrigation with saline water (1.9 dS m^{-1}) (Table 1) were higher, in general, in the plants with pumpkin rootstocks, regardless of scion type. These results (Figure 10

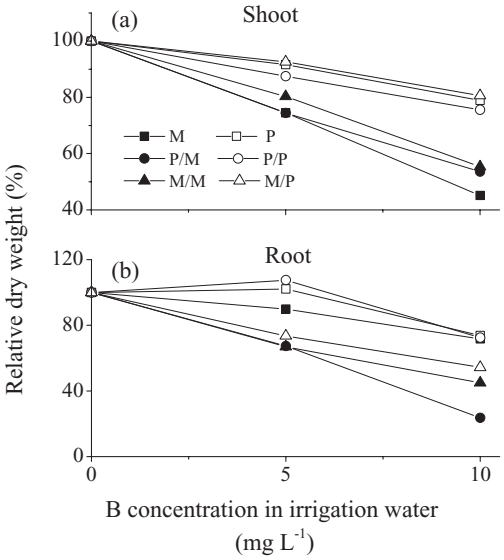

FIG. 10. Relative shoot (a) and root (b) dry weights of ungrafted pumpkin (P), ungrafted melon (M), melons grafted on their own rootstock (M/M), pumpkins grafted on their own rootstock (P/P), melons grafted on pumpkins (M/P), and pumpkins grafted on melons (P/M), as a function of boron concentration in the irrigation water. For each plant combination, the dry weight of shoot or root at zero B concentration in irrigation water was defined as 100% (following Edelstein *et al*., 2011).

and Table 1) suggested that in grafted plants, the root system, and not the scion, predominantly controls the salt and B stress response.

Several mechanisms have been proposed to explain the effects of tolerant rootstocks on improved productivity of salt-sensitive scions of vegetable crops (Colla *et al*., 2010): (i) salt exclusion by the root system which in turn decreases salt uptake by the plant; (ii) salt retention and accumulation in the rootstock tissues; (iii) accumulation of compatible osmolytes in the cytosol and organelles to balance the osmotic potential of the ions in the vacuoles; (iv) higher activity of enzymatic antioxidants, which also increases the activity of non-enzymatic antioxidants; (v) induction of hormones, mainly ABA and polyamines, due to higher rates of biosynthesis and lower degradation rates of polyamines. Several studies (e.g., Sykes, 1992; Walker *et al*., 2004, 2010; Hepaksoy *et al*., 2006; Musacchi *et al*., 2006; Ruiz *et al*., 2006; Lopez-Gomez *et al*., 2007; Mickelbart *et al*., 2007; Castro *et al*., 2009; Yetisir and Uygur, 2009; El-Nakhlawy *et al*., 2012) have found that the main mechanisms responsible for the increase in salt-tolerance of grafted vegetable plants are salt exclusion by the rootstock and retention of salts within its tissues. The effects of grafting on Na and Cl uptake and their distribution in plant tissues were measured and quantified by Edelstein *et al.* (2010, 2011) in a greenhouse experiment using six combinations of melon (cv. Arava) and pumpkin (cv. TZ-148) as described above. The Na concentrations in the shoots of the plants with melon rootstocks were high (390 to 414 mmol kg^{-1}), but very low (41 to 62 mmol kg^{-1}) with the pumpkin rootstocks, regardless of scion type. In contrast, shoot Cl^- concentrations were quite similar among the different scion–rootstock combinations. It was indicated (Edelstein *et al.,* 2010) that: (i) the pumpkin rootstocks exclude ∼74% of available Na, while there is nearly no Na exclusion by melon rootstocks; (ii) Na retention by the pumpkin rootstocks decreases its amount in the shoot by 46.9% as opposed to uniform Cl distribution throughout the plant.

TABLE 1
Dry weight of whole plant, shoots and roots of six different plant combinations: non-grafted pumpkin (P), self-grafted pumpkin (P/P), melon grafted on pumpkin rootstock (M/P), non-grafted melon (M), self-grafted melon (M/M), and pumpkin grafted on melon rootstock (P/M)

	Dry weight (kg $plant^{-1}$)		
Plant types	Whole plant	Shoot	Roots
		kg $plant^{-1}$	
P	0.1711 a*	0.1553 a	0.0158 a
P/P	0.1811 a	0.1688 a	0.0123 a
M/P	0.0822 b	0.0777 b	0.0045 b
M	0.0465 b	0.0428 b	0.0037 b
M/M	0.0641 b	0.0594 b	0.0047 b
P/M	0.1511 a	0.1396 a	0.0115 a

*Different letters in a column indicate statistically significant (at $\alpha = 0.05\%$) differences between the plant types.

C. Application of Non-Enzymatic Antioxidants

One of the earliest known responses of plants to salinity is a decrease in stomatal conductance as a result of the induced osmotic stress. The lower rate of CO_2 uptake by the plant, in this case, may lead to an over-reduction in ferredoxin by the photosynthetic electron transport system, and transfer of electrons from photosystem I (PSI) to oxygen-forming superoxide radicals via a process known as the Mehler Reaction (Hsu and Kao, 2003). This may initiate a chain reaction that produces more ROS that are harmful to the plant. This process is an outcome of the reduction of univalent molecular oxygen forming either superoxide, H_2O_2, hydroxyl radicals, or singlet oxygen (Wu *et al*., 2010). The accumulation of ROS may be detrimental to plant cells, as they may cause damage to cellular compounds and membranes (Davenport *et al*., 2003). Plants can develop a defense system against ROS consisting of non-enzymatic and enzymatic antioxidants (Davenport *et al*., 2003; Abdul Jaleel *et al*., 2007). The non-enzymatic antioxidants include mainly water-soluble glutathione, ascorbate, phenolics, lipid-soluble β-carotene and α-tocopherol. The enzymatic antioxidants include SOD, APX, GR, CAT, and POX. In some cases, the activities of these antioxidants are sufficient, but in many other cases, they may be insufficient. This raised the idea of using external application of non-enzymatic antioxidants to increase the plant's ability to defend itself against abiotic stresses, including salinity.

External application of antioxidants to salinity-exposed plants has been studied mostly by applying ascorbic acid to a number of plant species. Canola plants were grown in pots with a clay loam soil and irrigated daily with saline water containing 200 mM NaCl, and sprayed with 25 mM ascorbic acid or untreated (Dolatabadian *et al*., 2008). In the untreated plants, lipid peroxidation in leaves and roots increased protein and decreased chlorophyll contents in the leaves. In contrast, in ascorbic acid-treated plants, the activities of all antioxidant enzymes, except SOD, were significantly increased, while the increased protein in the leaves and roots and the decreased chlorophyll in leaves were limited (Dolatabadian *et al*., 2008). In bean plants, Dolatabadian and Jouneghani (2009) found that addition of 100 mM ascorbic acid to the nutrient solution alleviates the adverse effects of salinity, decreases the ROS activity in plant tissues, prevents lipid peroxidation, decreases malondialdehyde generation (the final product of membrane peroxidation), and raises the internal concentration of ascorbic acid which prevents ABA accumulation in plant cells.

In a field trial conducted over two consecutive years, the effects of several antioxidants—ascorbic acid, glutathione, α-tocopherol, and spermine—on wheat were investigated (Sakr and El-Metwally, 2009). The plants were grown in soil with salinity levels of 1.3, 6.0, and 9.5 dS m^{-1} in the saturated soil paste extract. While the high salinity decreased grain and stem + leaf weight of untreated wheat plants, spraying the plants or presoaking their seeds with the tested antioxidants alleviated the harmful effects of the salinity (Figure 11). This alleviation was

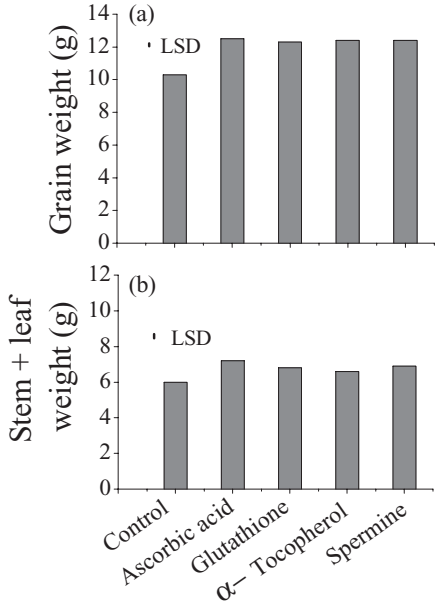

FIG. 11. Dry weight of grain yield (a) and stem + leaf (b) per wheat plant grown under salinity of 9.5 dS m^{-1} in the saturated soil paste extract following antioxidant treatment consisting of seed soaking prior to sowing and foliar spraying of ascorbic acid, glutathione, α-tocopherol, spermine, and control (untreated seeds and plant). LSD = least significant difference between means at $\alpha = 0.05$ level (following Sakr and El-Metwally, 2009).

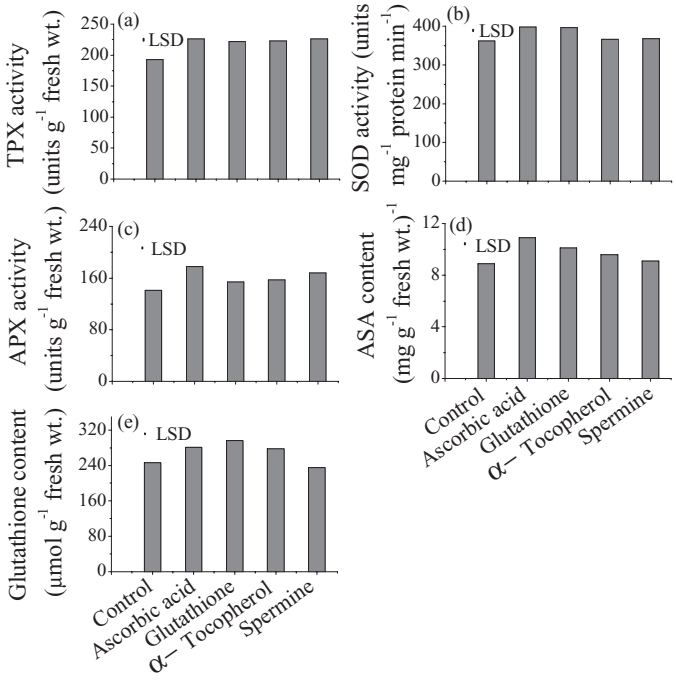

FIG. 12. Endogenous enzymatic antioxidant peroxidase activity (TPX) (a), non-enzymatic antioxidant superoxide dismutase activity (SOD) (b), ascorbic acid peroxidase activity (APX) (c), and content of ascorbic acid (ASA) (d) and glutathione in plant leaves (e) in wheat plants grown under salinity of 9.5 dS m^{-1} in the saturated soil paste extract for antioxidant treatment consisting of seed soaking prior to sowing and foliar spraying of ascorbic acid, glutathione, α-tocopherol, spermine, and control (untreated) seeds and plants. LSD = least significant difference between means at $\alpha = 0.05$ level (following Sakr and El-Metwally, 2009).

attributed to a rise in the internal non-enzymatic antioxidants and to the activity of enzymatic antioxidants (Figure 12). It was found in another trial with wheat grown hydroponically with 150 mM NaCl in the nutrient solution that application of 100 mg L^{-1} of ascorbic acid to the nutrient solution counteracts the adverse effects of the salinity on growth (Athar *et al*., 2008). This alleviation was associated with enhancement of CAT activity and photosynthetic rates. It also increased endogenous ascorbic acid concentration and K and Ca contents in the leaves, thus improving the K/Na ratio in leaf tissues.

Some studies (e.g., Ebrahim, 2005; Khafagy *et al*., 2009; Sakr and Arafa, 2009) investigated the effects of added ascorbic acid on plant growth and yield as related to antioxidation impacts. In a field trial with canola grown under salinity in the range of 10.1 to 14.6 dS m^{-1} in the soil solution, plant growth, yield and its components, including number of fruiting branches, fruits and seeds per fruit, and seed oil content, were determined in untreated and ascorbic acid-treated plants (Sakr and Arafa, 2009). In the untreated plants, all the determined parameters were decreased under salinity. In contrast, canola seeds soaked in a solution of 200 mg L^{-1} ascorbic acid prior to sowing and with an additional spraying of the plant foliage with this solution at 40 and 70 days after sowing showed enhancement in all

yield parameters as well as in the contents of photosynthetic pigments, proline and soluble sugars in the leaves. Khafagy *et al*. (2009) showed that soaking seeds of sweet pepper in ascorbic acid solution prior to sowing limits the reduction in plant height, root length and fresh and dry shoot weight, the increase in Na and the decrease in K content in the plant tissues of the mature pepper plants grown under saline conditions of 11.9 dS m^{-1} in the growth solution. In sugarbeets irrigated with saline water containing 100 or 200 mM NaCl, sucrose accumulation in the root and yield were suppressed (Ebrahim, 2005) as a result of an increase in the activity of sucrose-degrading enzymes, and a decrease in sucrose phosphate synthase activity. This led to an increase in hexose concentration in the storage roots (Ebrahim, 2005). In that experiment, application of 4 mM ascorbic acid to the sugarbeets alleviated the adverse effects of salinity. The added ascorbic acid increased the activity of sucrose synthase enzymes, which in turn abolished the adverse effects of salinity on sucrose accumulation and sugarbeet yield (Ebrahim, 2005).

Recent reports demonstrate the effects of ascorbic acid on salinity-exposed plants. For example, Younis *et al*. (2009a) found that germinating broad bean seeds in a medium containing 4 mM ascorbic acid results in the occurrence of particular novel proteins in seedlings which were exposed to salinity. Protein banding patterns of those broad bean seedlings showed different de novo protein bands with different molecular weights, and near absence of the major stress proteins. Younis *et al*. (2009a) assumed that these proteins induce protective changes in total amino acid content and composition. Anatomical changes were found by Arafa *et al*. (2009) in sorghum plants induced by ascorbic acid. Plants grown in nutrient solutions containing 25 to 100 mM NaCl and not treated with ascorbic acid decreased xylem and phloem tissue thickness, metaxylem vessel diameter and the main vascular bundle dimensions mainly at the high salinity level. However, immersing sorghum seeds in ascorbic acid or applying it to the foliage of sorghum plants counteracted the salinity's adverse effects (Arafa *et al*., 2009). Anatomical changes induced by ascorbic acid were also found in sweet pepper, where its application mitigated the salinity-induced decrease in thickness of the midrib region, spongy parenchyma, palisade layers and main vascular bundles (Khafagy *et al*., 2009).

Some studies showed induction of antioxidant activity in citrus plants under conditions of Na stress when roots were pretreated with 10 mM H_2O_2 for 8 h or 100 μM sodium nitroprusside for 48 h. The activities of leaf SOD, CAT, APX and GR in the treated citrus plants, grown in 150 mM NaCl solution, were increased, and the ascorbate redox state was partially prevented (Tanou *et al*., 2009). A quantitative assay and protein blotting analysis in this study also indicated that the NaCl-dependent protein oxidation is totally reversed by pretreatment with H_2O_2 (Tanou *et al*., 2009). It should be noted, however, that as of the present literature review, no other studies have shown induction of antioxidant activity by pretreatment with a strong oxidant such as H_2O_2. Therefore, this issue awaits further experimental confirmation.

D. Application of Plant Growth Regulators

Many studies have shown alterations in the level and action of plant hormones under salinity stress (e.g., Ashraf and Harris, 2004; Parida and Das, 2005; Kuznetsov *et al*., 2006; Tuteja, 2007; Kaya *et al*., 2009; Ashraf *et al*., 2010a). Exogenous application of natural hormones and synthetic growth regulators improved growth of tomato plants under salinity (100 mM NaCl in the growing media), raising K and decreasing Na content in the leaves and delaying their senescence (Albacete *et al*., 2008; Ghanem *et al*., 2008). All of these changes were related to decreased PSII activity, and changes in ABA, cytokinins, ethylene precursor and auxin contents in the leaves (Albacete *et al*., 2008; Ghanem *et al*., 2008), but the mechanisms underlying these effects remain unknown (Ashraf *et al*., 2010a).

1. Salicylic Acid

The use of SA to mitigate the adverse effects of salinity on plants has been recommended more than any other growth regulator. SA is well known for its medicinal properties, induction of flowering and retardation of petal senescence, and is associated with disease resistance. Foliar application of 1.0 mM SA to cucumber plants which were exposed to salinity levels of 0, 60, and 120 mM NaCl in the nutrient solution led to greater shoot and root fresh and dry weights, plant height, shoot diameter, leaf number, and leaf RWC than in untreated plants (Yildirim *et al*., 2008a). These authors also found that electrolyte leakage, which increases under salinity, was reduced in SA-treated plants (Yildirim *et al*., 2008a). Some important findings showing alleviation of salt effects on cucumber plants by SA application are presented in Figure 13. Similar results were obtained with strawberry, a salt-sensitive plant, when exposed to 35 mM NaCl in the nutrient solution and sprayed with SA solutions at concentrations ranging from 0.25 to 1.00 mM (Karlidag *et al*., 2009). In another study, Misra and Saxena (2009) found that exogenous application of SA to lentil plants grown in a saline medium of 100 mM NaCl significantly increases plant growth. Application of up to 1.0 mM SA to maize plants stressed with 40 mM NaCl enhanced growth significantly (Gunes *et al*., 2007). Similar results were obtained with *Phaseolus vulgaris*, when $\leq$ 0.5 mM SA solutions were sprayed on plants grown in a hydroponic solution containing 0, 100 or 150 mM NaCl (Palma *et al*., 2009). SA and its derivatives showed protection of maize plants from the detrimental effects of salinity, and increased dry weight and relative water content of the shoot (Tuna *et al*., 2007b). Germination was stimulated in wheat (Dolatabadian *et al*., 2009) and lentil (Misra and Saxena, 2009) after treating the seeds with 0.5 mM SA. The increase in germination was associated with enhanced cell division in the shoot and root.

In addition to SA's alleviation of adverse salinity effects on plant vegetative growth parameters, SA application has also been shown to improve productivity and yield quality of several

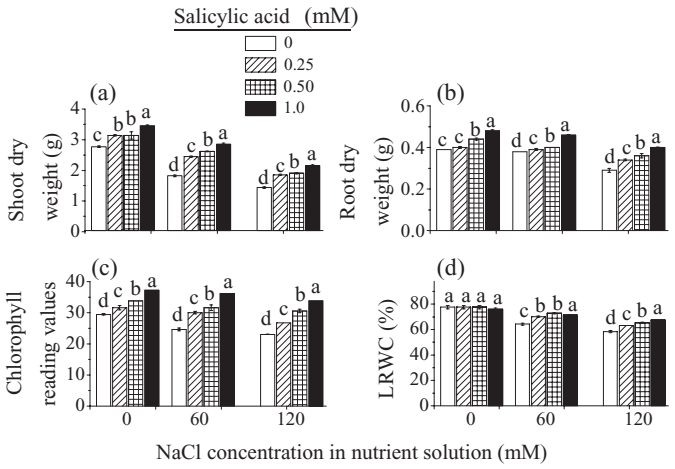

FIG. 13. Shoot (a) and root (b) dry weight per plant, chlorophyll reading values indicating its content in leaves (c), and leaf relative water content (LRWC) (d) of cucumber plants grown in 0, 60 and 120 mM NaCl in nutrient solution and treated with foliar application of 0, 0.25, 0.5, and 1.0 mM salicylic acid. Columns with different letters in each NaCl concentration and subfigure differ significantly at $\alpha = 0.05$ according to Duncan's Multiple Range Test (following Yildirim *et al*., 2008b).

plants (e.g., Arfan *et al*., 2007; Gunes *et al*., 2007; Tuna *et al*., 2007b; Noreen and Ashraf, 2010). Exogenous application of SA promoted growth and grain yield production of wheat plants under salt stress (Arfan *et al*., 2007). A foliar spray of 10–^{3} mM SA increased yield production of pepper plants grown under moderate salt-stress conditions in a greenhouse (Elwan and El-Hamahmi, 2009). This improvement was reflected in fruit number, average fruit weight, fruit yield, and fruit vitamin C and carotenoid contents (Elwan and El-Hamahmi, 2009). The dry weight of carrot storage roots, which was decreased by salinity, was positively affected by the addition of 0.5 mM SA to the growing media (Eraslan *et al*., 2007). Harmful effects of salinity on sunflower achene yield and oil characteristics were alleviated by exogenous application of SA at concentrations ranging from 100 to 300 mg L^{-1} (Noreen and Ashraf, 2010).

The mechanisms responsible for salinity-stress mitigation by SA are not completely clear. Arfan *et al*. (2007) claimed that SA application improves photosynthetic activity of wheat cultivars grown under saline conditions due to its effect on metabolic factors that control stomatal conductance and photosynthetic pigment production. Gunes *et al*. (2007) and Tuna *et al*. (2007b) showed an increase in the chlorophyll content of maize plants grown under salinity and treated with SA. In other findings, SA pretreatment of young tomato plants exposed to 100 mM NaCl increased the non-enzymatic antioxidant defense system and detoxifying capacity of the plant tissue (Szepesi *et al*., 2008). ROS scavenging became active and membrane damage was limited in wheat plants when their seeds were soaked in SA solution prior to sowing (Dolatabadian *et al*., 2009). A decrease in lipid peroxidation was also shown in SA-treated maize plants (Gunes *et al*., 2007). A rise in other antioxidants, such as carotenoids in carrots (Eraslan *et al*., 2007) and in maize (Gunes *et al*., 2007), was induced in salinity-exposed plants by exogenous application of SA. Misra and Saxena (2009) suggested another mechanism to explain SA amelioration of salinity-stress effects, which was demonstrated in lentils. They found that in shoots of lentil plants exposed to 100 mM NaCl, proline content was fivefold higher in plants treated with 0.5 mM SA than in untreated plants. Misra and Saxena (2009) explained the increase in proline as resulting from activity enhancement of enzymes involved in proline biosynthesis and its reduced oxidation. They also found a rise in GB content in the treated plants that maintained higher turgor pressure in the plant shoots, improving plant growth. In another study with maize plants, Gunes *et al*. (2007) found that under saline conditions, SA inhibits Na and Cl accumulation, but stimulates N, Mg, Fe, Mn, and Cu contents in the shoots. Another mechanism governing salinity-stress amelioration by SA was suggested by Tari *et al*. (2002). They found that tomato plants, which were exposed for an extended period to 100 mM NaCl and to 1 × 10–^{4} to 0.5 mM SA in the nutrient solution, used the Na accumulated in the plant tissues to function as osmolytes with no detrimental effect. All of the above-described beneficial results of SA application indicate that SA indeed alleviates symptoms of salinity stress in plants, although no clear dominant mechanism has been suggested for this phenomenon.

2. *Brassinosteroids*

Brassinosteroids (BRs) have garnered much interest due to their effects of increasing plant tolerance to salt stress and improving development under salinity (e.g., Özdemir *et al*., 2004; Ali *et al*., 2007). Ashraf *et al*. (2010a) presented several studies on BRs applied to either the growing medium or as a foliar spray. Application of 24-epibrassinolide (EBR) to the growing media accelerated seed germination and seedling growth of sorghum under osmotic stress (Vardhini and Rao, 2003). Tabur and Demir (2009) added EBR to the growing media of barley plants grown under salinity of 0.35 to 0.4 M NaCl and found a significant decrease in the mitotic index and the number of chromosomal abnormalities as compared to the untreated plants. Application of 4 μM BR to a nutrient solution containing 150 or 300 mM NaCl ameliorated the negative effects of salinity on the levels of nucleic acids, soluble proteins and proline, and peroxidase activity (Bera *et al*., 2006).

Application of 0.052 or 0.104 μM BR to 1/2 strength Hoagland solution containing 120 mM NaCl was most efficient at increasing grain size and yield of wheat (Ali *et al*., 2008). However, application of EBR via the growing medium is not straightforward, because it requires optimization of the EBR concentration and duration of the treatment. Application of EBR at the wrong concentration might be harmful to the plants due to a dose-response relationship (Ashraf *et al*., 2010a). Moreover, the quantity of BR required to obtain optimal concentrations in the soil or growing media may be high and costly. In addition, application of BR to the soil may involve some uncertainty due to its degradation by microorganisms, or leaching from the root

zone by the irrigation water. Spraying bean plants, which were grown in 150 mM NaCl added to washed sand, with 5 μM EBR at 15 days after transplanting detoxified the stress effects, and increased antioxidative enzyme activity and the level of proline (Rady, 2011). Electrolyte leakage and lipid peroxidation were decreased, and membrane stability and RWC were increased. In another trial with beans (Shahid *et al*., 2011), the deleterious effects induced by salinity were reduced when seeds were treated with EBR before or after NaCl application.

A presowing seed treatment with BR under saline conditions improves germination and seedling establishment, and increases the shoot and root biomass and seed yield of several crops, including rice, barley, wheat, beans and pepper (Ashraf *et al*., 2010a). Another protective action of presowing treatment with BR is control of the level of other hormones, as it prevents the decrease in cytokinin level and lowers the level of the stress-induced hormone ABA (Avalbaev *et al*., 2010). It can be concluded from these results that the proper concentration of the sprayed BR solution and the correct timing of its application, as related to the plant's growth stage, should be predetermined for specific plants and local agronomic and environmental conditions.

3. *Abscisic Acid*

Salinity stress can also be alleviated in plants using more common hormones, such as ABA, although information on this approach is minimal. A rise in the internal level of ABA under salt stress was found to contribute to membrane integrity, enabling plants to regulate uptake and transport of ions (Parida and Das, 2005). These authors also found that the inducible genes of ABA play an important role in the mechanism of salt-tolerance in rice plants. Different responses to various modes of external ABA application were found in potato plants under saline conditions (Etehadnia *et al*., 2008); application of a single dose of ABA enhanced mainly the vertical growth of the plant, whereas multiple and gradually increasing doses of ABA increased lateral growth and water content of the shoot. Etehadnia *et al*. (2008) also grafted ABA-deficient mutant plants onto a rootstock with known elevated ABA levels; the rootstock added significant ABA doses to the scion and alleviated the plant's response to salinity. Gurmani *et al*. (2007) documented an ameliorative effect on salinity-exposed wheat plants when their seeds were presoaked in a solution containing 10–^{2} mM ABA for 24 h. In that study, a significant decrease in Na and increase in K contents in the wheat leaves, and a rise in grain yield were found. Improved growth of bean plants grown under saline conditions was observed when the plants were treated by external addition of ABA before being exposed to the saline stress (Khadri *et al*., 2007). In this case, ABA improved growth parameters, normalized nodule weight, restored nitrogenase activity, limited the transport of Na to the shoots, and resulted in a higher K/Na ratio in the plant leaves.

4. *Indole Acetic Acid, Kinetin, and Benzyl Adenine*

Foliar application of IAA and kinetin (Kin) to maize plants exposed to 100 mM NaCl in the nutrient solution alleviates most of the adverse effects of salinity, such as the decrease in plant biomass production, chlorophyll content and RWC (Kaya *et al*., 2010). These two hormones, mainly at a concentration of 2 mM, also increased proline accumulation in the leaves, maintained membrane permeability, and increased Ca and P contents in the leaves and roots; however they also reduced the activities of antioxidant enzymes in the plants (Kaya *et al*., 2010). Application of IAA and kinetin as a presowing seed treatment did not improve the salinity tolerance of mature maize plants.

In contrast, using kinetin as a presowing seed treatment significantly alleviated the salt-inhibited seed germination of saltgrass (Shahba *et al*., 2008) and of *Halogeton glomeratus* (Khan *et al*., 2009). Saline conditions inhibited transcription of the Zm-EXPAI gene in cells of maize leaves (Veselov *et al*., 2008), but IAA activated ZmEXPAI, leading to regulation of cell expansion and growth of the maize plants. Shah (2011) also showed a reduction in the adverse effects of salinity in *Nigella sativa* plants watered with Hoagland solution containing 75 to 150 mM NaCl, and sprayed with 10 μM kinetin. Leaf RWC and area, stomatal conductance, chlorophyll content and aminolevulinic acid dehydratase (ALA-D) activity were all increased, and oxidative stress was alleviated, resulting in higher yield than for untreated stressed plants. Gurmani *et al*. (2007) found that BA has ameliorative effects similar to those of ABA on plants under salinity stress.

5. *Gibberellins*

Application of Gibberellic acid (GA) has also been found to counteract some of the adverse effects of salinity, such as those on dry matter production, chlorophyll content and RWC of maize plants (Tuna *et al*., 2008b) and linseed plants (Khan *et al*., 2010). Application of 50 mg L^{-1} of GA to the nutrient solution induced accumulation of osmoprotectants such as proline and GB, induced the antioxidative defense system, improved membrane permeability and elevated nutrient levels. Application of GA was either by foliar spray or as an additive to the nutrient solution, which was shown to be more effective when added together with Ca salts, but is probably not practical under actual growing conditions.

6. *Jasmonates*

Jasmonates are generally considered mediators of defense-response signals, such as in flowering and senescence, but they can also play an important role in plant salt tolerance. For example, Hilda *et al*. (2003) found that jasmonate levels in plant tissues are higher in salt-tolerant vs. salt-sensitive tomato cultivars. Kang *et al*. (2005) applied 30 μM jasmonic acid 24 or 48 h after exposure of rice plants to saline solution (20 to 40 mM NaCl); this resulted in decreased Na uptake, increased photosynthetic rate and a more negative leaf water potential.

Consequently, the inhibition of biomass production under saline conditions was partially relieved. It should be noted that there is a lack of studies on the ameliorative effect of jasmonic acid on crop production under saline conditions, and additional studies on this topic are warranted.

7. Polyamines

Polyamines are known as elicitors of diverse physiological activities in plants, such as cell division, tuber formation, root initiation, flower development, and fruit ripening; they also have beneficial effects on abiotic stress tolerance (Hopkins, 1999). Their polycationic nature limits their transport within the plant, and thus their roles in plants are not truly hormonal. Nevertheless, the polyamines participate in several metabolic pathways, and they interact with negative charges in cells, such as phosphates, phospholipids, nucleic acids and carboxylic protein groups (Kuznetsov *et al*., 2006). The use of natural polyamines to protect plants against various stressors, including salinity, has been documented by various investigators (e.g., Ashraf and Harris, 2004; Verma and Mishra, 2005; Kuznetsov *et al*., 2006; Zhu *et al*., 2006; Ndayiragije and Lutts, 2007), but the mechanism governing these processes has not been documented. Ashraf and Harris (2004) indicated that external addition of three polyamines: putrescine, spermidine and spermine, to pea seedlings attenuates the inhibitory effects of salt stress. Verma and Mishra (2005) found that a concentration of 0.1 mM putrescine in Hoagland solution significantly reverses the reduction in seedling growth of Indian mustard (*Brassica juncea* L.) grown under saline conditions by limiting the increase in superoxide and H_2O_2 levels, lipid peroxidation and membrane leakage of cells, inducing antioxygenic enzymes, and increasing the level of glutathione and carotenoids in the leaves.

Salinity-induced damage to plasma membranes can be ameliorated by spermidine treatment (Roy *et al*., 2005). Plasma membranes isolated from roots of salt-sensitive and salt-tolerant rice seedlings and treated with 150 mM NaCl for 16 h revealed severe inhibition of H-ATPase activity, whereas in the presence of 1 mM spermidine, this activity was significantly recovered. Ndayiragije and Lutts (2007) found that 10 μM putrescine improves the growth and yield of rice plants grown under saline condition (30 mM NaCl in the nutrient solution). These effects of putrescine application on yield and growth of rice plants were associated with an increase in K/Na ratio in shoots and roots, and with improvement of assimilation rates due to increased stomatal conductance (Ndayiragije and Lutts, 2007). The decrease in Na accumulation in shoots was claimed to be a consequence of its binding to exodermal intercellular spaces and cortical cells in the roots, as shown in spermidine-treated barley plants (Zhu *et al*., 2006). Low accumulation of K and Na was found in endodermal cells and stellar parenchyma of roots in salinity-stressed plants treated with spermidine. In cucumber plants grown under saline conditions, addition of spermidine to the nutrient solution alleviated membrane damage, mainly in the root system, and increased the photosynthetic rate of the plants (Duan *et al*., 2008) and performance of antioxidant enzymes in the plant cells (Duan *et al*., 2008; Du *et al*., 2010) due to induced expression and enhanced activity of POD, SOD and CAT.

Differences between species might explain the contradictory findings on the salinity-alleviating effects of spermine. Sakr and Arafa (2009) and Sakr and El-Metwally (2009) indicated that the salinity-induced depression of growth and yield of canola and wheat plants is counteracted by spermine due to increased activity of antioxidant enzymes. On the other hand, Ndayiragije and Lutts (2007) claimed that there are no protective effects of spermine on salt-treated rice plants. Ren *et al*. (2007) found that the compound 2-furan-2-yl[1,3]dioxolane, which was presented as a novel plant growth regulator, enhances salinity tolerance of wheat plants by increasing the number and fresh weight of roots and dry weight of shoots. It was claimed to have no mutagenic potential, but the mechanism governing its action is not known.

E. Application of Compatible Solutes

Many plant species growing under environmental stress conditions accumulate compatible solutes in their tissues, mainly GB and proline, which contribute to their osmotic adjustment. Cuin and Shabala (2005) suggested that the role of compatible solutes in plant tissues under saline stress is not limited to osmotic adjustment; they have additional regulatory functions, including protection against ROS and maintaining cytosolic K homeostasis by preventing NaCl-induced leakage of ions. Many plant species accumulate insufficient concentrations of compatible solutes for those functions, and there are some species that do not accumulate such solutes at all (Ashraf and Foolad, 2007). This raised the notion that concentrations of proline or GB should be increased in plants grown under saline conditions. Much effort has been spent on breeding and genetic engineering of plants to produce high concentrations of compatible solutes, but the practical achievements in these cases are still low. Another approach is to apply these solutes to plants by external means.

Application of proline or GB to wheat, rice, corn, barley, bean, soybean, cotton, tobacco, potato, and tomato plants grown under saline conditions enhances the growth and yield of the treated plants as compared to untreated ones (Ashraf and Foolad, 2007). These positive effects of proline and GB application were attributed to the osmoprotection and cryoprotection conferred by these solutes, and to the increased activity of antioxidative enzymes, such as SOD and POX. In addition, accumulation of Na and Cl decreased in the shoot and increased in the roots of plants treated with proline or GB (Ashraf and Foolad, 2007). Reduced accumulation of Na and Cl was also found in tomato plants grown in nutrient solution containing 135 mM NaCl, when 1 or 5 mM GB or 1 mM proline was added to the solution (Heuer, 2003).

Additional studies emphasized the beneffical effect of proline and GB on seed germination, growth and yield of plants grown under saline conditions. Nawaz and Ashraf (2007) and Ashraf *et al*. (2008a) found that foliar application of 50 and

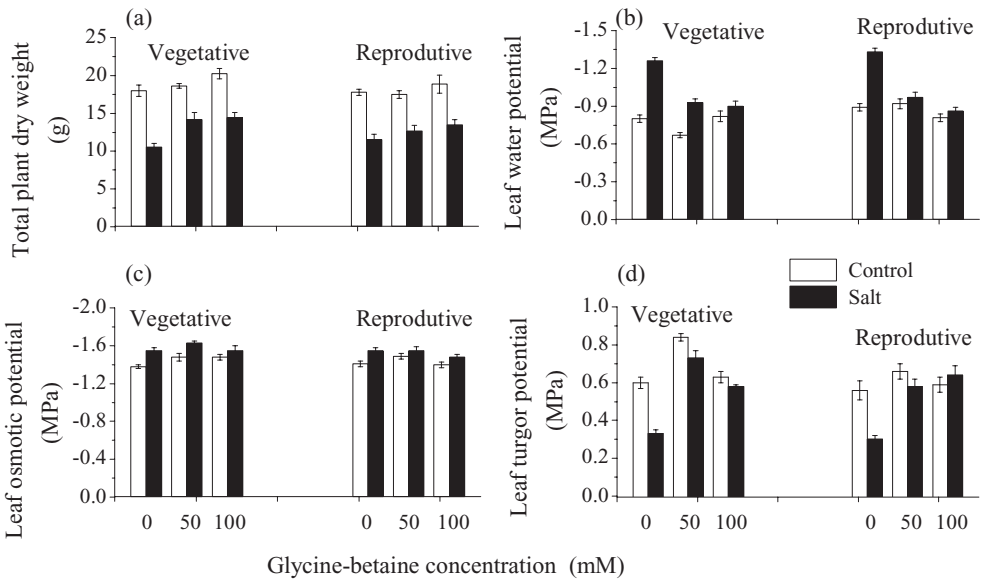

FIG. 14. Total plant dry weight (a) and leaf water (b), osmotic (c), and turgor (d) potentials of maize plants (cultivar C-20) grown under high (salt) and low (control) salt stress after foliar application of 0, 50, and 100 mM glycine betaine. SEMs are presented by vertical bars (following Nawaz and Ashraf, 2007).

100 mM solutions of GB during the vegetative growth stage of maize and wheat counteracts the salt-induced reduction in plant growth and yield. This beneficial effect of GB was associated with a marked decrease in osmotic potential and an increase in turgor potential in the leaves (Figure 14). Abbas *et al*. (2010) found that foliar application of 50 mM GB increases the growth and yield of two eggplant cultivars that were grown under saline conditions. Foliar application of 50 and 100 mM GB in solution improved the growth of wheat cultivars grown under field conditions with salt stress of 15 dS m^{-1} by increasing photosynthetic rates (Raza *et al*., 2006). Proline also ameliorated the adverse effects of salinity on fruit yield of melon (Kaya *et al*., 2007) and cucumber (Huang *et al*., 2009), and on growth of young olive trees (Ben Ahmed *et al*., 2010). Germination percentage of sorghum seeds under saline conditions was increased when the seeds were presoaked in GB solution, and seedling growth was further improved when sprayed with GB (Arafa *et al*., 2009). Water status in maize (Ashraf and Foolad, 2007), olive (Ben Ahmed *et al*., 2010) and cucumber (Huang *et al*., 2009) grown under saline conditions was improved after these plants were sprayed with 10 to 33, 25 to 50, and 100 mM GB, respectively. An increase in germination was also found in seeds of the desert shrub *Halogeton glomeratus* when 1 mM proline was added to the saline germination solution containing <900 mM NaCl (Khan *et al*., 2009).

The following mechanisms have been suggested for the protection of plants against the harmful effects of salts by externally applied compatible solutes: (i) mitigation of oxidative-stress damage to membrane transporters (Cuin and Shabala, 2008); (ii) maintenance of membrane permeability, as shown for melon plants (Kaya *et al*., 2007); (iii) increased activity of POX, as shown for cucumber plants (Huang *et al*., 2009); (iv) increased activities of the antioxidative enzymes SOD, CAT and APX, and decreased activity of polyphenol oxidase, even under the high external salinity of 200 mM NaCl, as shown for young olive trees (Ben Ahmed *et al*., 2010); (v) an increase in SOD activity, decreased lipid oxidation and increased chlorophyll content, as shown for common ice plants (Shevyakova *et al*., 2009); (vi) reduced K flux out of the root cells, maintaining cytosolic K homeostasis, as shown for barley plants (Cuin and Shabala, 2005); (vii) increased concentrations of Ca, K and N in leaves, as shown for melon plants (Kaya *et al*., 2007).

Several investigators (e.g., Yang and Lu, 2005; Raza *et al*., 2006; Abbas *et al*., 2010) pointed out that increased photosynthetic rates, which were probably a result of water status improvement which increased stomatal conductance, are most likely responsible for the enhancement of growth and production of plants under saline stress. The mechanism of salt-stress alleviation of GB-treated plants was also studied by proteomic analysis of radicle and hypocotyl proteins of tomato seedlings grown in nutrient solution with 120 mM NaCl and 5 mM GB (Chen *et al.,* 2009). Twenty-three salt-stress-response proteins could be identified and classified into six groups in the salinity-exposed plants. Salinity-induced inhibition of plant growth could be alleviated with GB via an increase in six proteins' expressions in the salt-tolerant cv. Patio, and two proteins' expressions in the salt-sensitive cv. F144, to over twofold their expression in untreated stressed plants.

Although application of proline and GB through the root system requires larger amounts of material than application by foliar spray, the former is the most common application method (Ashraf and Foolad, 2007). Soaking seeds in solutions of

proline or GB prior to their sowing has also been used in several cases (Ashraf and Foolad, 2007). The effective concentrations of GB and proline and the timing and frequency of their application depend on the specific plant species to be treated (Ashraf and Foolad, 2007). It is important to emphasize, however, that practical use of GB and proline at optimal concentrations and frequencies under field conditions is costly and may not be feasible. Therefore, the use of crude extracts containing compatible solutes, such as sugarbeet extracts, has been recommended as a replacement for GB (Abbas *et al*., 2010).

An increase in the concentration of trehalose, another compatible solute, which can serve as an osmoprotectant against salt stress in plant tissues, could be obtained by an inhibitor of trehalase activity (Lopez *et al*., 2009). In *Medicago truncatula* plants, which were grown in sterile vermiculite and irrigated with nutrient solution containing 0 or 50 mM NaCl, increasing trehalose in the root nodules by validamycin A application increased the plant's dry biomass (Lopez *et al*., 2009). Seckin *et al*. (2009) used mannitol, a sugar alcohol that is not synthesized by higher plants, as an osmoprotectant, and found that exposing young wheat seedlings to 100 mM mannitol for 24 h and then subjecting them to 100 mM NaCl in the nutrient solution results in improved root growth, increased activities of antioxidant enzymes such as SOD, POX, CAT, APX and GR, and reduced membrane lipid peroxidation. It should be noted, however, that the number of studies on the use of trehalose and mannitol to alleviate adverse salinity effects is limited.

F. Foliar Application of Nutrients

Foliar application of mineral nutrients (N, P, K) has been found to mitigate the adverse effects of salinity in several crops. The most effective nutrient is K, which has been tested in various forms. Akram *et al*. (2009b) found that foliar application of various salts containing 1.25% K to sunflowers plants grown in 150 mM NaCl in the rooting media increases plant K content, root and shoot dry weight, and achene yield and size. The salts K_2SO_4, KH_2PO_4, KNO_3, and K_2CO were more effective than KCl or KOH. In another study, Akram *et al*. (2009a) found that spraying $\geq$130 mM K_2SO_4 on sunflowers grown under similar saline conditions increases photosynthesis and transpiration rates, stomatal conductance, WUE, leaf turgor, and plant growth and yield, but the contents of Na, Cl, Mg, Ca, P, and N in the plants were not affected by the K_2SO_4 application. In a later report, Akram *et al*. (2011) recommended foliar application of KH_2PO_4 and showed its effectiveness in improving growth and yield of sunflower plants grown in pots under similar conditions. The improved growth was associated with enhanced photosynthetic capacity, WUE and RWC.

Foliar application of 10 mM KH_2PO_4 to eggplants grown under saline conditions (50 mM NaCl in the nutrient solution) improves plant growth and yield, lowers Na content in the fruits, and increases the content of K, Ca and P in all plant parts, and sugar in the fruits (Elwan, 2010). It was also found that spraying 500 mg L^{-1} KCl solution on cotton plants irrigated with saline water (6.2 dS m^{-1}) enhances the plants' vegetative and reproductive production; this enhancement was much more pronounced when the application of KCl was combined with 500 mg L^{-1} NH_4NO_3 (Jabeen and Ahmed, 2009). In a recent paper, Jabeen and Ahmed (2012) showed that a mixture of 250 mg L^{-1} KNO_3 and 5 μg L^{-1} H_3BO_3 and Fe-EDTA sprayed on sunflower and safflower plants irrigated with water containing sea salts at EC levels of 4.8 or 8.6 dS m^{-1} partially minimizes the salt-induced damage; fresh and dry biomass, number and weight of seeds and amount of oil in sunflower and safflower plants increased, and the effect was independent of their growth under non-saline or saline conditions. Akram and Ashraf (2009) also found that a combined spray of K and N ($\sim$250 mM KNO_3) on sunflower grown under saline conditions of 150 mM NaCl in the growing media increases chlorophyll content, CO_2 assimilation rates, quantum yield, leaf turgor, vegetative growth, and K and N contents in the leaves. Zheng *et al*. (2010) confirmed these findings in their study and in addition, they showed an improvement in flour and dough quality from wheat plants grown with 100 mM NaCl in the growing medium, and sprayed with 10 mM KNO_3.

The effect of foliar application of N as $Ca(NO_3)_2$ in solution on alleviation of the adverse effects of salinity in cowpea plants exposed to 50 mM NaCl in the nutrient solution was studied by (Murillo-Amador *et al*., 2006). Application of $Ca(NO_3)_2$ increased chlorophyll fluorescence, but did not improve stomatal conductance, transpiration rates, net photosynthesis or intercellular CO_2 concentrations. Yildirim *et al*. (2009) found that foliar application of $Ca(NO_3)_2$ and KNO_3 increases the dry weight and leaf RWC in strawberry plants grown in a mixture of soil and peat at a 1/1 (v/v) ratio and irrigated with water containing 40 mM NaCl.

Foliar application of urea was also found to overcome the adverse effects of salinity. Younis *et al*. (2009b) found that spraying a 3 to 5% urea solution before and after transplanting of lettuce plants grown under saline conditions of $\leq$7 dS m^{-1} increases the growth parameters and metabolite contents in the treated plants, but application of urea at concentrations $\geq$6% significantly decreases these same parameters. An increase in proline, as well as in glycine content was shown in lettuce plants whose foliage was sprayed with increasing concentrations of urea (Hasaneen *et al*., 2008). Del Amor and Cuadra-Crespo (2011) found that broccoli plants, grown in coconut fibers and irrigated with saline water containing 40 mM NaCl by drip irrigation, and sprayed with 10 g L^{-1} urea solution, maintain their gas-exchange parameters and leaf N and Na contents at levels similar to those in plants grown under non-saline conditions. However, this beneficial effect of urea application was not found in broccoli plants irrigated with water containing 120 mM NaCl (del Amor and Cuadra-Crespo, 2011). In mulberry trees, which were grown in pots and exposed to salinity levels between 1.58 and 19.2 dS m^{-1} in the growing media, the addition of nitrogenous *Azotobacter chroococcum* biofertilizer by foliar application was more effective at improving tree growth and development than soil application (Vijayan *et al*., 2007).

G. Application of Other Chemicals and Microalgae Extracts

The need to increase plant tolerance to salinity has led researchers to study the effects of various chemicals, such as metabolic intermediates, fungicides and other toxic materials, on plants exposed to salinity. Several such chemicals have demonstrated positive effects on plant growth and production or on basic physiological activities related to salinity tolerance.

1. Plant and Microalgae Extracts

Wheat plants irrigated with water containing 10 or 20% seawater and treated with water extract of the microalgae *Spirolina maxima* and *Chlorella ellipsoidea* increases the carotenoid, tocopherol, and protein contents in the grains, associated with increased antioxidant activity (Abd El-Baki *et al*., 2010). Abbas *et al*. (2010) found that application of sugarbeet extract to eggplant counteracts the adverse effects of salinity by increasing photosynthetic rates, stomatal conductance, leaf K and Ca contents, plant growth and yield, and decreasing leaf Na and Cl content. As the sugarbeet extract contains substantial amounts of GB, it may be applied as a source of GB for improvement of plant growth and production under saline conditions (Abbas *et al*., 2010).

Wheat germ agglutinin, a lectin extracted from wheat germ, is normally used for the binding of various metabolites. Bezrukova *et al*. (2008) found that in 4-day-old wheat seedlings pretreated with wheat germ agglutinin, which were then placed in a solution containing 2% NaCl for up to 24 h, salinity-induced ROS activity, lipid peroxidation, and electrolyte leakage are abolished.

2. Metabolic Intermediates

Aminolevulinic acid (ALA)—a precursor of chlorophyll and heme biosynthesis—at a concentration of between 0.01 and 10 mg L^{-1} promoted the germination of pakchoi seeds stressed at a salinity level of 150 mM NaCl (Wang *et al*., 2005). Increased growth and improved water relations were found in oilseed rape (*Brassica napus* L.) exposed to 100 to 200 mM NaCl in the nutrient solution after foliar application of 30 mg L^{-1} ALA (Naeem *et al*., 2010). ALA application also partially prevented the decrease in shoot and root growth, chlorophyll content, net photosynthesis, and leaf water potential caused by salinity, and increased the leaf contents of all nutrients except Mn and Cu. Zhang *et al*. (2006) found that addition of 0.3 to 3.0 mg L^{-1} ALA to the propagation medium of potato plantlets propagated from single node sections, containing 0.5% NaCl, ameliorates the adverse effects of salinity. The number, diameter, and fresh weight of microtubers increased. The ameliorative effects of ALA application were attributed to protection of membranes in the microtubers against oxidative damage; for instance, POX activity was increased by 73% and that of polyphenol oxidase by 28% as compared with the untreated plants (Zhang *et al*., 2006). ALA was also used to improve salt-tolerance of date palm seedlings subjected to seawater at concentrations of up to 30 dS m^{-1} by application of 0.08% ALA-based fertilizer (Youssef and Awad, 2008). The seedlings showed increased photosynthetic rates, total chlororophyll and chlorophyll a contents and biochemical factors limiting gas exchange and assimilation rates.

The isoflavone genisten served as an antioxidant to mitigate salt stress in plants. Miransari and Smith (2007) found that application of genisten at concentrations ranging from 5 to 29 μM increases the yield of soybean grown under saline conditions by up to 21%. In this case, the disrupted signal between the plant itself and the nodules was eliminated, and this probably increased nodulation and N_2-fixation in the treated plants.

3. Fungicides and Phytotoxins

Triadimefon is a fungicide used for controlling plant diseases, such as powdery mildew and rust, which has also been used to mitigate salinity's adverse effects. Jaleel *et al*. (2008) found that addition of 5 mg L^{-1} triadimefon to the irrigation water mitigates the adverse effects of salinity on germination percentage, chlorophyll content, non-enzymatic antioxidant content, antioxidant enzyme activity, and growth of *Withania somnifera* plants grown in washed sand irrigated with water containing 40 mM NaCl.

Similar results were documented for another fungicide - paclobutrazol - applied to cowpea (*Vigna unguiculata* L.) subjected to 100 mM NaCl in the irrigation water (Manivannan *et al*., 2008) or to vinca (*Catharanthus roseus* L.) subjected to 80 mM NaCl (Jaleel *et al*., 2007). Stem elongation, plant fresh and dry weight and leaf area were inhibited in both plants under salinity. In cowpea, the activities of SOD, POX and CAT and in vinca, those of ascorbic acid and glutathione were also decreased. When 15 mg L^{-1} paclobutrazol was added to the irrigation water, both enzymatic and non-enzymatic activities were significantly enhanced. Paclobutrazol was also added to *Nerium oleander* plants irrigated with saline water (70 mM NaCl) at a rate of 30 mg per plant (Banon *et al.,* 2005). The salinity-induced leaf defoliation and reduced root dry weight were decreased by paclobutrazol. The contents of Na and Cl in stems and roots and of Cl in the leaves were decreased due to reduced uptake, and osmotic adjustment was improved through the accumulation of organic compounds.

The fungicide hexaconazole was found to ameliorate salinity injury in canola seedlings grown after seed soaking and initial soil wetting with a solution of 200 mM NaCl. Hexaconazole, which was applied at a concentration of 50 mg L^{-1}, increased shoot and root growth, dry weight, chlorophyll content, protein content and antioxidant enzyme activity (Akbari *et al*., 2011).

Fusicoccin is synthesized by the fungus *Fusicoccum* which is normally toxic to plants. It induces an irreversible binding of 14-3-3 protein to the C terminus of the H^+-ATPase, thus activating H^+ pumping. Shahba *et al*. (2008) studied the effect of 10 μM fusicoccin added to germination solutions containing 0, 15 or 30 dS m^{-1} NaCl on the germination of saltgrass (*Distichlis speciata*), and found that the addition of fusicoccin significantly enhances germination. Similar results for saltgrass germination

were obtained under application of 30 mM thiourea (Shahba *et al*., 2008). Khan *et al*. (2009) found that application of fusicoccin and thiourea also alleviates germination inhibition of the desert shrub (*Halogeton glomeraus*) under salinity rates of 300 to 900 mM NaCl in the germination solution.

Coronatine is a phytotoxin produced by several plant-pathogenic bacteria. Xie *et al*. (2008) found that pretreatment of cotton seedlings with 0.01 μM coronatine solution confers salinity tolerance to mature cotton plants grown hydroponically in 150 mM NaCl. Coronatine increased the scavenging activities of POD, CAT, GR, and 1,1-diphenyl-2-picrylhydrazyl, and consequently the production of ROS was reduced, membrane peroxidation and electrolyte leakage were prevented, and seedling growth was increased.

V. CONCLUDING REMARKS

There are two main approaches to alleviating the adverse effects of salinity on agricultural crops: (1) development of salt-tolerant cultivars by screening, conventional breeding, and genetic engineering, and (2) the traditional approaches that involve treatment and management of the soil, plants, irrigation water, and plant environment. Success has been limited using the first approach under commercial growing conditions, mainly because salt-tolerance traits in plants are very complex. The present paper reviews, analyzes, and discusses the traditional approaches related to: (i) improvement of the plant environment, (ii) inoculation of the crop plant with bacteria or fungi, and (iii) treating the plants themselves.

The plant environment can be improved by decreasing salt content and concentration and enhancing nutrients composition and their concentrations in the root zone, and by controlling the plants' aerial environment. Salt content in the root zone can be reduced mainly by the following means:

a) Under irrigation conditions, the dominant technique is salt leaching, based on adding a sufficient amount of water beyond that required for evapotranspirative demands. This technique increases the yield of different crops, such as citrus, avocado, sugarcane, tomato, maize, wheat, rice, and pepper, grown under various saline conditions. The guideline for calculating the *LR* for salt leaching is based, in general, on steady-state conditions, disregarding salt precipitation and preferential flow, and assuming that salt concentration of the soil solution at any point in the root zone is constant. Recently, new *LR*-calculation models have been suggested that take into account soil/water interactions as a dynamic process. Switching the calculation of the *LR* from steady-state to dynamic decreases the estimated *LR* values, leading to substantial water savings and a reduction in chemical movement toward the groundwater, with no reduction in crop yield. Advanced irrigation systems can provide important means for reducing the salt content in the root zone. Leaching of salts from the root zone is more efficient and crop yields under saline conditions are higher by irrigation with a drip system than by surface or sprinkler irrigation, due to the more favorable distribution of salts in the irrigated field.
b) In many areas, such as the Mediterranean region, winter rainfall can leach the salts accumulated in the soil profile during the irrigated summer season. The effectiveness of this leaching is controlled by soil water-holding capacity and rainfall properties, such as its distribution. Salt leaching is more effective under concentrated rainfall during the winter season (pre-season salt leaching) than under rainfall distributed throughout the year (mid-season leaching). It should be emphasized, however, that the leaching technique under irrigation and rainfall conditions can only be applied under adequate drainage conditions, which allow leaching of the salts below the root zone.
c) Growing high-salt-tolerant primer or companion plants. The idea in this approach is that the primer and companion plants will absorb significant quantities of salt from the soil, and consequently establish a less salted rootzone for more sensitive crops.This approach was tested in several studies with trefoil (*Lotus corniculatus*), canola, lucerne, safflower, sulla, and tall wheatgrass as primer plants, and *Salsola soda* as the companion plant. It was found that the primer and companion plants decreased the salinity level in the rootzone and increased crop yields, but the companion plant was only useful for relatively low salinity ($\sim$4 dS m^{-1} in the substrate solution).
d) Covering the soil surface, mainly with plastic sheet or mulch. The soil cover is designed to reduce evaporation from the soil surface, and thus decreases the salt accumulation in the upper soil layer. It was found that covering the soil with a plastic sheet, wheat, maize or rice straw, gravel, or pine needles decreased, in general, the average salt concentration in the upper soil layer (0–40 cm) and increased crop yield. However, the recommended amount of mulch for soil cover needs to be further studied in the field, under local and specific conditions.

The use of suitable fertilization to improve nutrient composition and concentrations in salted root zones has been documented in many studies. K, N as NO_3^-, and Ca are the major fertilizers that most improve the performance of crops, such as potatoes, lettuce, barley, strawberry, pepper, endives, tomato, and sugarcane, under saline conditions. The added K counteracts the deleterious effects of Na by lowering Na uptake by the plants. Increasing NO_3^- concentration in the soil solution might decrease Cl^- uptake by the plant under saline conditions, as a result of competition between NO_3^- and Cl^- anions for their uptake by the plant roots. The mechanisms suggested to be responsible for the alleviation of salinity damage by Ca application in the growing media are (i) supplemental Ca, mostly as $CaSO_4$, which affects membrane permeability, leading to higher concentrations of Ca, K, and N, and a lower concentration of Na in the leaf cells; (ii) increasing GB and proline contents in the leaves and callus of several plant species leads to osmotic

adjustment of the plants; (iii) increased Ca in the leaves, that enhances the activity of antioxidant enzymes, such as SOD, POX, and CAT, leading to increased protection of cells in the treated plants.

Improving the plants' aerial environment mitigates the adverse effects of salinity on growth and crop production primarily by the following means:

a) Increasing aerial CO_2 concentration significantly enhances photosynthesis and WUE of various plants under saline conditions. This enhancement is attributed to mechanisms that reduce water loss, form thicker cell walls and cuticle, and increase chlorophyll and carotenoid contents, ROS detoxification activity, and the expression of enzymes responsible for more active detoxification of ROS and of β-ATPase, which are efficient in ion transport and homeostasis in plants. In some cases, however, elevated CO_2 concentration stimulates plant growth under saline conditions mainly by improving leaf water status.
b) Misting in a greenhouse increases the air humidity and decreases the vapor-pressure deficit and air temperature which, in turn, increase day time stomatal conductance, net CO_2 assimilation rates, and water uptake in various plants. These parameters cause the leaf water potential to be less negative, and enhance the turgor, leaf area, dry matter production, and yield of the plants.
c) Shading the greenhouse decreases incoming radiation intensity and the aerial temperature, and consequently increases the growth and fruit yield of different plants grown under saline conditions. However, the interactions between air temperature and salinity, their effects on the growth and yield of various crops, and the mechanism responsible for this phenomenon require further verification and clarification.

Overcoming the adverse effects of salinity and increasing the productivity of various plants can also be achieved by inoculating the roots with salt-tolerant bacteria, as described below:

a) Bacterium-mediated tolerance of plants to salt stress has been shown for several crops, such as peas, maize, groundnut, chickpeas, faba beans, lettuce, pepper, and tomato. The most effective rhizobacteria were *Pseudomonas putida* and *Pseudomonas fluorescens*, isolated from the rhizosphere of wheat grown in salt-affected soils.
b) Mycorrhizal fungi can increase salt-tolerance in plants. For example, the ectomycorrhizal basidiomycete *Piriformospora indica* was found to be salt tolerant and to induce tolerance in host monocot and eudicot plants. Studies conducted on barley as the host inoculated with this fungus

TABLE 2
Treatments (Trt.) and their effects on physiological activities in plants (denoted by an x) under saline conditions

	†Physiological activities in plants																		
*Trt.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A	x	x		x	x				x	x	x			x				x	x
B	x		x	x							x	x	x	x					x
C	x	x		x		x	x			x				x				x	
D			x											x					
E	x	x										x						x	
F	x	x										x	x						x
G	x			x					x	x	x			x					
H	x	x	x	x	x				x	x	x		x		x	x	x		
I		x								x	x	x							
J		x				x	x		x	x	x	x			x		x		
K	x					x	x	x		x		x							

Note. *Treatments list; †Physiological activities list.

A - Soil fertilization with K; B - Soil fertilization with Ca; C - Soil fertilization with N; D - Soil fertilization with P; E - Soil fertilization with S; F - Micronutrients fertilization; G - Organic manure application; H - Si application; I - Soil mulching; J - Increasing aerial CO_2; K-Increasing air humidity; 1 - Reduction in Na and Cl uptake & transport to shoot; 2 - K uptake enhancement; 3 - Ca uptake enhancement; 4 - Increasing of osmolytes synthesis; 5 - Carbohdrates accumulation & osmotic adjustment; 6 - Controling stomatal & leaf conductance; 7 - Improvement of plant water status; 8 - Transpiration rate reduction; 9 - Increasing photosynthetic pigment level; 10 - Increasing photosynthetic rate; 11 - Activity enhancement of enzymatic & non-enzymatic antioxidants; 12 - Increasing scavenging or detoxification of ROS; 13 - Improvement of plasma-membrane stability & function; 14 - Enhancement of N, P, K uptake; 15 - Activity stimulation of enzymes; 16 - Controling the levels of planr hormones; 17 - Diminishing the increase in leaf modulus of elasticity; 18 - Synthesis enhancement of amino acid & N metabolism; 19 - Reduction in blossom-end-rot

TABLE 3
Treatments (Trt.) and their effects on physiological activities in plants (denoted by an x) under saline conditions

	†Physiological activities in plants																			
*Trt.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
A	x	x	x	x		x	x	x	x	x					x		x			
B		x		x	x					x		x					x			x
C	x	x	x	x	x		x	x	x	x				x	x		x		x	
D			x			x		x			x	x		x		x	x	x		
E	x	x		x		x	x		x	x							x			
F	x	x		x	x			x	x	x		x								x
G	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
H	x	x				x	x	x	x	x	x	x		x						x
I	x	x				x	x	x	x									x		
J	x	x	x	x		x	x	x	x	x	x	x	x		x	x			x	x

Note. *List of treatments; †List of physiological activities.

A - Inoculation with bacteria; B - Inoculation with mycorrhiza; C - Inoculation with arbuscular mycorrhiza; D - Seed priming; E - Plant grafting; F - Antioxidant application; G - Growth regulators application; H - Compatible solutes application; I - Nutrient foliar application; J - Other chemicals application; 1 - Reduction in Na and Cl uptake & transport to shoot; 2 - K uptake enhancement; 3 - Ca & Mg uptake enhancement; 4 - Increasing of osmolytes synthesis; 5 – Carbohdrates accumulation & osmotic adjustment; 6 - Controling stomatal conductance; 7 - Improvement of plant water status; 8 - Increasing photosynthetic pigment levels; 9 - Increasing photosynthetic rate; 10 - Activity enhancement of enzymatic & non-enzymatic antioxidants; 11 - Increasing scavenging or detoxification of ROS; 12 - Attenuation of lipid peroxidation; 13 - Increasing carotenoids and toocopherol content; 14 - Improvement of plasma-membrane stability & function; 15 - Decreasing electrolyte leakage; 16 - Activity stimulation of enzymes; 17 - Controling the levels of planr hormones; 18 - Increasing cell diviation rate; 19 - Increasing nodules number and N fixation; 20 - Synthesis enhancement of amino acid & N metabolism

showed enhanced activity of antioxidants, such as DHAR, and increased the concentration of ascorbic acid. The activity of additional antioxidants, such as GR, CAT, APX, DHAR and MDHAR, was also increased in salinity-exposed barley roots colonized by *P. indica.* The most responsive antioxidants were DHAR, MDHAR and CAT. Roots of forest trees exposed to salt and mycorrhiza showed higher accumulation of ABA and SA, known as stimulators of salinity tolerance, and a decrease in auxin and jasmonic acid. The K/Na ratios, carbohydrate accumulation and root cell volume were also increased in mycorrhiza-colonized plants. The main beneficial effects of the mycorrhizal fungi were attributed to increased P uptake during early growth stages and increased K uptake during later stages, leading to increased K/Na ratio in the roots, and decreased uptake of Na and Cl.

Other plant treatments that can be effective at reducing damage due to salinity are:

a) Seed treatment prior to germination (seed priming) contributes to metabolic repair in seeds, increased germination, reduced time of imbibition and induced osmotic adjustment. For example, priming of melon seeds in an 18 dS m^{-1} solution decreased the negative effects of irrigation with saline water. In those plants, the content of K and Ca in the leaves increased, and this increase prevented the toxic effects of the salinity. Seed priming with plant hormones, such as ABA, BA, IAA, and GA, is also effective in inducing salt-tolerance. Use of large seeds was found effective at overcoming salinity problems in several mature plants.
b) Grafting of salt-sensitive plants onto salt-tolerant rootstocks can alleviate the adverse effects of salinity. In this case, the rootstocks increase the tolerance of the grafted plants mainly by preventing accumulation of Na and Cl in the leaves.
c) Application of antioxidants, such as ascorbic acid, to salinity-exposed plants increases their resistance to salinity. Some studies have shown that these antioxidants increase the activities of leaf SOD, CAT, APX and GR which prevent the damage caused by salinity.
d) Application of plant growth regulators such as SA, BRs, ABA, IAA, Kin, GA, jasmonates, and polyamines can alleviate the adverse effects of salinity on vegetative growth and yield quantity and quality. The main effects of these growth regulators are in activating some antioxidant enzymes, decreasing Na and Cl uptake, increasing K/Na ratio in the shoot, and increasing photosynthesis.
e) Foliar application of mineral nutrients (N, P, and K) can mitigate the adverse effects of salinity, with the most effective nutrient being K. Application of these nutrients increases the chlorophyll content, CO_2-assimilation rate, quantum yield, leaf turgor, vegetative growth, and K and N contents in the leaves.

f) Application of plant extracts, metabolic intermediates, fungicides, and phytotoxins is effective at increasing salt-tolerance of several plants. These chemicals increase nodulation, N_2 fixation and enzyme activities, and decrease electrolyte leakage, thereby increasing seedling growth.

Several physiological activities in plants are known to be inhibited by salinity, resulting in the adverse effects of salinity on plant growth and productivity. To mitigate these adverse effects, the relevant physiological activities need to be restored. The different treatments and means discussed in the present review that have effects on physiological activities in the plants are summarized in Tables 2 and 3. Plant treatments that involve application of growth regulators, compatible solute, and other chemicals, inoculation of plant roots with bacteria and arbuscular ectomycorrhiza, and application of K fertilizers and Si to the soil under saline conditions stimulate a large number of physiological parameters ($\geq$10) in the salinity-exposed plants (Tables 2 and 3). In contrast, soil fertilization with P and S stimulate fewer than five physiological parameters in the plants (Tables 2 and 3).

Nearly all of the studies published on alleviation of salinity stress in crop plants by traditional approaches have concentrated mostly on one specific treatment. Hardly any of the studies have made an attempt to explore the simultaneous effects of two or more treatments known to have a positive effect on salinity alleviation. Since the mechanisms underlying the improvement of salinity tolerance by the various treatments are not fully understood, it is quite possible that different treatments have additive or even synergistic effects. The salinity-incurred damage to plants may thus be decreased much more effectively, to the benefit of plant growth and production under salinity. Studies along these lines are promising and await further investigation. Such studies may also shed light on the various mechanisms by which the treatments overcome salinity barriers.

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