Saline agriculture in Mediterranean environments

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Abstract

Salinization is increasingly affecting world's agricultural land causing serious yield loss and soil degradation. Understanding how we could improve crop productivity in salinized environments is therefore critical to meet the challenging goal of feeding 9.3 billion people by 2050. Our comprehension of fundamental physiological mechanisms in plant salt stress adaptation has greatly advanced over the last decades. However, many of these mechanisms have been linked to salt tolerance in simplified experimental systems whereas they have been rarely *functionally* proven in real agricultural contexts. In-depth analyses of specific crop-salinity interactions could reveal important aspects of plant salt stress adaptation as well as novel physiological/agronomic targets to improve salinity tolerance. These include the developmental role of root *vs.* shoot systems respect to water-ion homeostasis, morphological vs. metabolic contributions to stress adaptation, developmental processes *vs.* seasonal soil salinity evolution, residual effects of saline irrigation in non-irrigated crops, critical parameters of salt tolerance in soil-less systems and controlled environments, response to multiple stresses. Finally, *beneficial* effects of salinization on qualitative parameters such as stress-induced accumulation of high nutritional value secondary metabolites should be considered, also. In this short review we attempted to highlight the multifaceted nature of salinity in Mediterranean agricultural systems by summarizing most experimental activity carried out at the Department of Agricultural Engineering and Agronomy of University of Naples Federico II in the last few years.

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Introduction

Salinity is one of the major environmental constraints that limit crop productivity and quality. The United Nations Food and Agriculture Organization estimated that approximately 20% of irrigated lands is affected by increasing salinity (Rozema and Flowers, 2008). The competition for fresh water in agricultural, domestic and industrial uses, mainly due to the growing population and climate changes, is further contributing to salinization (United Nations, 2009). Arid and semiarid regions are more exposed to this phenomenon since in these climatic zones high evapotranspiration rates, irrigation and reduced rainfall all concur to salt accumulation in the uppermost soil layers, where root development mostly occurs (Munns, 2005). Salinization does not pertain only to extreme environments and/or southern regions of the world, however. In Europe, 26 countries have reported cases of salinization with higher frequency in Mediterranean coastal areas (Flowers, 2004). Although soil salinization could be delayed through proper irrigation management (Rhoades *et al*., 1992) it cannot be avoided. Consequently, the progression of salinization is increasingly jeopardizing productions of irrigated lands, the most active agricultural areas of the world (Royal Society, 2009).

Historical background

In order to identify proper strategies to improve agricultural management in salinized areas it is essential to understand how salinity develops in the soil and how plants react to salt stress. The effects of salinization on agricultural crops have been discussed in a vast body of literature (Hasegawa *et al*., 2000) although in early years, inhomogeneous experimental conditions, unknown species-specific variability and insufficiently developed experimental techniques have somehow hindered progress in this field. In order to compare salinity tolerance in different plant species, standardization criteria were introduced by Maas and Hoffman (1977) who described the response of glycophytes to salinity by plotting the relative yield as a continuous function of root zone salinity. Based on this model, it was possible to categorize different species respect to two specific parameters, namely the tolerance threshold (i.e. the maximum soil salinity that does not reduce yield below that obtained under non-saline conditions) and the slope (i.e. the rate of yield decay beyond the tolerance threshold). Although the classification of Maas and Hoffman was mostly intended to provide a practical guideline in terms of crop choice and water management in saline agriculture (Rhoades *et al*., 1992), it also pointed to different physiological bases that could determine variable responses to salinity. This was an important step towards the comprehension of the fundamental biology of plant salt tolerance.

The Maas-Hoffman model was proven to be quite useful for a first-level ranking of crop salt tolerance (Maas and Hoffman, 1977; Maas and Grattan, 1999). However it turned out to be rather unstable respect to environmental factors that could interact with and affect general growth and/or plant responses to salinity. Plant exposure to different root-zone temperatures (Dalton *et al*., 1997), solar radiation (Dalton *et* *al*., 2001) and aerial CO_2 levels (Maggio *et al*., 2002) may affect both threshold and slope of the Maas-Hoffman salt response curve and consequently weaken the comparative purpose of this model. It was specifically argued that a simple relationship between relative yield and root zone salinity could not uncouple general plant growth responses from specific salt tolerance properties (Dalton *et al*., 2000). These observations pointed to the need of identifying new indexes that were more stable to environmental variables and eventually shed some light on the intrinsic physiological basis of plant salt tolerance. The salinity stress index (SSI) proposed by Frank Dalton and collaborators (Dalton *et al*., 1997) complied with these requirements. The SSI also identified a threshold-slope behavior of the plant response function to salinity, yet it was at the same time an environmentally invariant measure of plant salt tolerance because it integrated biochemical and variable physical parameters in the soil-plant-air continuum, which control salt loading to the shoot and simultaneously affect transpiration and growth (Dalton *et al*., 2000).

Subsequently, the water day stress index (WDSI) has also been proposed to assess plant response to salinity and further elucidate the complex relationship between plant water requirements and stress adaptation at whole-plant level (Katerji *et al*., 2000).

A major breakthrough towards *standardization* in salinity research has been the introduction of plant model systems that allowed us to link the extensive number of observations on the physiology of plant salt tolerance to a genetic basis (Zhu, 2000; Pardo, 2010). In the last 20 years, the use of Arabidopsis and, more recently, Arabidopsis relative model systems (Inan *et al*., 2004; Orsini *et al*., 2010b) has considerably contributed to improve our understanding of the fundamental molecular and physiological mechanisms in plant salt stress adaptation (Zhu, 2002).

We know today that the genetic variation defining different tolerance levels controls four major physiological processes: i) water/ion homeostasis; ii) hormone regulation and metabolic adjustment; iii) growth control and iv) injury control (Bressan *et al*., 2009). Genes involved in critical steps of these four processes have been isolated and transferred via genetic engineering to improve plant stress tolerance (Chinnusamy *et al*., 2005). Despite the polygenic nature of salinity and abiotic-stress tolerance in general, it has been demonstrated that salt tolerance can be improved by single-gene manipulation. Overexpression of *SOS1*- (Shi *et al*., 2003) and *NHX1*- (Zhang and Blumwald, 2001; Zhang *et al*., 2001), two genes involved in the control of Na^+ homeostasis, has allowed plant growth and flowering at 200 mM NaCl, a concentration that would be lethal for most cultivated crops. Additional targets for improving salt stress tolerance through genetic engineering include osmolytes overproduction (Karakas *et al*., 1997; Sheveleva *et al*., 1997; Sakamoto *et al*., 1998), potentiating the antioxidant system (Samis *et al*., 2002) and overexpression of transcription factors that could confer resistance to multiple abiotic stresses by simultaneous activation of several stress tolerance genes (Kasuga *et al*., 1999). Single-gene control of stress tolerance mechanisms was also demonstrated in *Thellungiella halophila* (salt cress), a halophytic Arabidopsis relative model system (Inan *et al*., 2004). Ethane-methylsulfonate (EMS) mutagenesis of salt cress seeds, followed by screening for reduced salinity tolerance, resulted in the isolation of putative mutants with loss of extreme tolerance, which behaved similarly to the glycophytic *Arabidopsis thaliana* (Inan *et al*., 2004).

Although the experimental results obtained so far are encouraging and have laid solid ground for stable crop salt tolerance improvements, the number of transgenic crops that have undergone to field trials is to date rather small (Xue *et al*., 2004). Major advancements can be expected upon identification of more efficient alleles of candidate genes (Quintero *et al*., 2002; Maggio *et al*., 2006), genetic engineering of newly identified components, combinations that would potentiate more than one above mentioned critical physiological mechanisms and identification of novel control mechanisms (Chinnusamy and Zhu, 2009).

The possibility of using halophytes as potential crops for extreme environments has been reconsidered also in light of recent advancement in molecular techniques that may accelerate the selection of halophytic species that could best adapt to *productive* cultural systems (Rozema and Flowers, 2008).

It is unquestionable that the elucidation of fundamental molecular and physiological responses to salinity is instrumental to improving crops salt tolerance. Nevertheless, there has been little effort to frame these responses into specific cultural scenarios (Maggio *et al*., 2003a). In Mediterranean areas, the diversity of agricultural systems underlies the existence of different *salinities* that may have quite diverse effects on crop yield and quality. The Department of Agricultural Engineering and Agronomy at the University of Naples Federico II has been engaged since 1988 (Barbieri *et al*., 1994) in a long-term research activity aimed at elucidating the complexity of crop-salinity interactions in specific agricultural contexts. In the following, we attempted to summarize some of the results achieved so far and to highlight future research needs.

Short- and long-term salinization

Often overlooked have been the differences between short-term/temporary effects of salinization vs. long-term effects, the latter referred either to single irrigation seasons or multiple years. Summer irrigation of vegetable crops may cause variable salinization of the root zone that will dynamically evolve throughout the growing season. The magnitude of the damage to the crop will depend on the coincidence between salt toxicity levels and sensitivity of specific phenological stages to salt stress (Lutts *et al*., 1995; Hasegawa *et al*., 2000). Seasonal/temporary salinization can be partially controlled by fulfilling appropriate leaching requirements (Rhoades *et al*., 1992). However, at advanced salinization, permanent modifications of the soil physical-chemical properties will occur (Katerji *et al*., 1992; De Pascale *et al*., 2003c). These will further damage normal plant growth and consequently crop yield/quality. In Mediterranean areas, residual salinity and salinity-induced soil deterioration may affect both irrigated spring/summer crops and non-irrigated winter crops if autumn/winter rainfall is insufficient to counteract summer salinization by leaching the toxic ions below the root zone (De Pascale and Barbieri, 1997; De Pascale *et al*., 2005). Repeated irrigation with salinized water, associated with reduced winter rainfall, may lead to a substantial modification of the soil properties. Salinized soils often have higher water content because of a reduced water uptake, transpiration and development of salt stressed plants as well as reduced soil permeability due to the formation of surface seals (Rhoades *et al*., 1992; De Pascale and Barbieri, 1995). In the experimental field at the University of Naples Federico II Agronomy farm (latitude 43°31_N; longitude 14°58_E), a clay-loam soil (42% sand, 27% silt, 31% clay, trace amounts of lime) that had been irrigated with 1% w/v NaCl (171 mM) for ten years presented typical characteristics of alkaline-saline soils with decreased structure index, high water content, poor root zone aeration, surface crusting, pH ≥8.0 and remarkably reduced water infiltration rate (12 mm h^{-1} in non salinized control plots *vs.* 1 mm h^{-1} in soil irrigated with 1% NaCl). This was mostly associated to prevalence of sodium on the adsorption complex, which causes deflocculation of the clay particles and consequent reduction of soil permeability (Hachicha *et al*., 2000; De Pascale *et al*., 2005). In spite of EC_e fluctuations during the year (high EC in summer and low EC in winter), monitoring of the winter soil EC has revealed a yearly linear increase of 0.46 dS m^{-1} over a 10-year period up to an EC of 6.1 dS m^{-1}, indicating that the fall-winter rainfall was insufficient to contain salt accumulation caused by 1% NaCl summer irrigation (De Pascale and Barbieri, 2000).

Short- and long term-responses should also be considered within each growing season. In Mediterranean areas, salt stress typically overlaps with midday water stress, which is experienced when plant transpirational rates are unable to cope with high VPDs. In these conditions, crops have to overcome both daily exposure to hyperosmotic stress and seasonal effects due to salt accumulation in the root-zone (Maggio *et al*., 2004). In tomato, we have highlighted different physiological responses to short- and long-term stress adaptation. Indeed plants that were more efficient in diurnal/daily osmotic adjustment did not perform as well, in terms of osmotically adjustment, over the entire growth season (Maggio *et al*., 2004). To date, it is still unclear which physiological mechanism is most critical respect to specific phenological stages and crop yield. This is not a trivial issue since physiological and metabolic adaptation mechanisms that may have an important function at certain developmental stage may be less effective in others (Sakamoto and Murata, 2002). When salinization occurs as seasonal phenomenon (i.e. summer irrigation for horticultural crops) critical salinity levels may be reached in proximity of fruit onset (tomato). At this stage, mechanisms of ion re-translocation/accumulation in older leaves may be more effective than ion compartmentation and/or exclusion for coping with an excessive tissue concentration of toxic ions (Pardossi *et al*., 1998; Maggio *et al*., 2005). Higher Na^+ accumulation in older leaves of salinized plants has been observed and functionally linked to a specific stress adaptation program (Amzallag, 2002; Zhu, 2002; Zhang and Blumwald, 2001). The activation of specific stress protection mechanisms respect to the developmental/seasonal stage has been studied in tomato (Maggio *et al*., 2007b). Experimental evidence suggests that at salinity higher than 2.5 dS m^{-1} (the tolerance threshold for tomato - Maas and Hoffman, 1977), *a second* physiological threshold (EC of 9.6 dSm^{-1}, corresponding to 88.5 mM Cl^+) may activate a functional metabolic shift between different adaptation mechanisms. Physiologically, this transition is likely mediated by the abscisic acid (ABA) level, which at moderate stress (before the second stress threshold) is responsible for the control of short-term adaptation processes such as stomatal regulation and cellular homeostasis (Wilkinson and Davies, 2002). At advanced salinization (after the second tolerance threshold), higher ABA tissue concentrations may be involved in the control of organ adaptation processes, which will eventually lead to structural changes, including functional modifications of the root-to-shoot ratio (Maggio *et al*., 2007b).

Functional morphologies in stress adaptation

Genetic engineering for improved plant salt tolerance has mostly focused on downstream components of stress adaptation, namely ion exclusion/compartmentation and osmolytes accumulation (Maggio *et al*., 2001; Bressan *et al*., 2008). Less explored have been many morphological traits that could also be important in stress adaptation, including root and stomatal features. Unequivocal data on root architectures/morphologies that can benefit stress adaptation in saline environments are currently unavailable. Unlike drought stressed plants that generally expand their root systems (Cuartero and Fernàndez-Muñoz, 1999), salt stressed plants do not seem to respond to the same stimuli. Cabbage plants exposed to comparable levels of saline and drought stresses, in terms of soil water potentials, decreased their shoot/root ratio much less in the former compared to the latter (Maggio *et al*., 2005). It has been argued that large root/shoot ratios may be detrimental in saline environments since they would enhance the accumulation of toxic ions into the shoot and consequently anticipate the onset of the salt tolerance threshold (Dalton *et al*., 1997; Munns, 2002). In line with this view, it has been demonstrated in citrus that a reduced root-to-shoot ratio may improve salinity tolerance (Moya *et al*., 1999). As previously discussed, structural modifications such as the control of shoot vs. root growth should be seen as part of a dynamic adaptation process in which plant physiological/metabolic responses evolve in parallel with plant development, soil salinization and atmospheric parameters throughout the growth season (Maggio *et al*., 2004; 2005). In spite of a large number of genes that are know to affect root morphologies, these concepts have not been confirmed or negated in plant model systems or different crops through gain- or loss-of-function experiments (Maggio *et al*., 2001; Morant *et al*., 2010).

Another trait in salinity tolerance, which has not received sufficient attention, is the stomatal control of transpirational water fluxes. Non-transpiring plants (or plants with a reduced transpiration rate) may overcome transitory salinity stress partly because the uploading of toxic ions to the shoot will be restricted and the oncoming of toxicity levels in photosynthesizing tissues will be delayed. Reduced transpiration due to low stomatal conductance will also reduce CO_2 uptake, however. Plants with closed stomata may tolerate hypersomotic stress but they will not grow (Maggio *et al*., 2003b). During transitory stress events (midday water stress), a prompt stomatal closure may preserve tissue turgidity and prevent wilting. However, under permanent stresses, such as those caused by repeated saline irrigation or salinized soils, the control of stomatal aperture may be not an effective target to improve plant growth and yield. *In vitro* isolation of Arabidopsis mutants with increased salinity tolerance confirmed this *tolerance-growth* physiological trade-off. Mutants with a nonfunctional 9-cis-epoxicarotenoid dioxygenase (NCED) had a reduced level of stress-inducible ABA. *nced* plants were able to germinate and grow in Petri plates under saturated atmosphere but were hypersensitive to salinity in greenhouse, due to their inability to close their stomata (Ruggiero *et al*., 2004). It has been demonstrated in non-stressed plants that overexpression of *NCED* may increase the tissues ABA concentration and decrease stomatal conductance without affecting CO_2 assimilation and biomass accumulation (Thompson *et al*., 2007). While the *NCED* mediated stomatal regulation was proven to improve water use efficiency in non-stressed plants, its effect remains elusive respect to stress tolerance.

ABA is a major player in the control of plant stress adaptation, however it is only one component of an orchestrated hormonal control (Ross and Neill; 2001; Nemhauser *et al*., 2006). Other hormones are involved in the fine regulation of plant growth vs. adaptation that may have important practical implications in terms of yield and product quality (Weiss and Ori, 2007). Once again, the relative role of different hormones may be more or less important respect to both the level of stress experienced and the developmental stage. In tomato, different levels of endogenous GA3 and ABA on water fluxes may reduce or enhance plant salt tolerance (Maggio *et al*., 2010). It is therefore important to consider the actual level of stress to which crops are exposed since the control of hormonal balance, via genetic engineering or chemical treatments, may have positive effects at low and moderate salinity whereas it may have undesirable effects at moderate to high salinity.

The modulation of ABA levels to overcome moderate and/or transitory stresses could still find practical applications in greenhouse cultivation (De Pascale *et al*., 2003b; Maggio *et al*., 2010) where it is possible to adapt the environment to the actual plants needs. In principle, climatic control of the VPD and physiological control of stomatal conductance may be adjusted in order to *uncouple* water loss and CO_2 uptake. This would consent to improve WUE and/or stress tolerance in controlled environments (De Pascale and Maggio, 2008).

More recently, stomatal traits have been proven to critically affect WUE. In absence of stress, it has been demonstrated that low stomatal density reduces transpirational water fluxes (Zhang *et al*., 2008) and improves water use efficiency (Masle *et al*., 2005).

Interaction with other abiotic/biotic stressors

The co-existence of multiple stresses is common in nature. Typically, in Mediterranean environments drought, heat and saline stress overlap. In addition, plants that suffer abiotic stresses are more susceptible to pathogens/pests attacks, which will further exacerbate damages and eventually compromise the final yield (Cheong *et al*., 2002; Xiong and Yang, 2003; Bostok, 2005).

Although there is a great variability of plant stress response to diverse cultural environments, the simultaneous occurrence of multiple stresses adds an extra level of complexity for the identification of *field* stress tolerance mechanisms. In this respect, comparative analysis of drought and salt stress responses may reveal physiological specificities and important practical implications. Celery is a relatively salt tolerant species that can be irrigated with saline water (up to 8.5 dS m^{-1}) with acceptable yield losses. Nevertheless, celery plants exposed to a level of water stress that is comparable, in terms of soil water potential to a respective saline stress, are unable to effectively cope with it (De Pascale *et al*., 2003a). We do not know if such response is a general one or specific to some species. However, it indicates that plant responses to drought and saline stress can be only partially superimposed (De Pascale *et al*., 2007). This may have important agronomic implications since the specific physiological response will determine the economic threshold based on which decisions on irrigating or not with saline water may be taken (i.e. choosing to expose plants either to moderate salt stress or to moderate water stress). Similar studies conducted in Southern Italy with pepper have indicated that an ECw of 4.4 $dS{\cdot}m^{-1}$ is a critical economic threshold for saline irrigation of this species (De Pascale *et al*., 2003c).

From a different perspective, it is worth emphasizing that molecular/physiological responses to diverse stresses may also overlap and confer cross tolerance, if potentiated. A few examples exist in the literature on multiple tolerances to different abiotic stresses. Overexpression of transcription factors has been proven to confer simultaneous tolerance to salinity, drought and freezing (Kasuga *et al*., 2004). Molecular components that control both biotic and biotic stress responses have been identified, also. Overproduction of osmotin in potato (Liu *et al*., 1994) and tomato (Goel *et al*., 2010) conferring tolerance to *Phytoptora infestans* and osmotic stress, respectively, is a classical example of this kind. Broad tolerance to biotic and abiotic stresses can be achieved by overexpressing transcription factors that have been shown to coordinately control the function of multiple stress responsive genes (Agarwal *et al*., 2006; Oh *et al*., 2007; Takumi *et al*., 2008). Additional examples include the function of secondary metabolites. In tomato, overexpression of prosystemin confers tolerance to afid attacks (Corrado *et al*., 2007) and salinity (Orsini *et al*., 2010a). Prosystemin transgenic tomato plants have been shown to perceive a less stressful environment when exposed to saline stress, indicating that a constitutive activation of wound responses, mediated by high prosystemin levels, can pre-adapt plants to further stresses.

The partial stomatal closure often presented by Mediterranean crops, including those of salinized coastal regions, is detrimental for achieving the maximum potential yield. However, it may protect agricultural crops from other environmental stressors. Phytotoxic levels of ozone (O3) concentrations have been documented across Europe (Fagnano and Maggio, 2008b; Fagnano *et al*., 2009). These levels are much higher in Italy (Forlani *et al*., 2005; Fagnano and Maggio 2008a), Greece (Saitanis, 2008) and Spain (Gimeno *et al*., 1994) compared to North-Central Europe (EEA, 1996; 2003) and are likely to further increase in the years to come (Sitch *et al*., 2007). Since ozone enters into the plant through the stomata, the variability of plant response to ozone exposure depends on a number of factors that affect stomatal conductance. Experiments carried out in open top chambers (OTC) (Fagnano *et al*., 2004) at the University of Naples Federico II have documented reduced ozone damages in salt stressed plants (Maggio *et al*., 2007a; Maggio *et al*., 2009b). This partial protection was associated to a reduced stomatal conductance caused by salt stress and, possibly, to the production of antioxidant molecules that is also salt-stress induced and further counteracts ozone damages (Wellburn and Wellburn, 1996; Ranieri *et al*., 2000; Maggio *et al*., 2007a; Maggio and Fagnano, 2008). These observations have raised a need for revising current models for predicting crop ozone damages, since these rely on plant response functions based on ozone exposure (Fuhrer *et al*., 1997) rather than uptake, which may conceivably provide more reliable information on the actual toxicity levels (Fiscus *et al*., 2005; Pleijel *et al*., 2007).

Effects on product quality

The effects of salinity on quality parameters of the commercial products are less known respect to those on yield. Nevertheless, many high-nutritional value secondary metabolites with acknowledged properties in the prevention of important human diseases, such as cancer and cardiovascular pathologies, accumulate in fresh fruits and vegetables in response to salinity and other environmental stresses (De Pascale *et al*., 2001). Tomato yield can be reduced to 50% at 8 dS m^{-1} (Maggio *et al*., 2004), yet irrigation with saline water can significantly improve both sugar and organic acid content of cherry tomatoes (De Pascale *et al*., 2007) and the flavour of processed tomatoes (Mitchell *et al*., 1991). Contrasting results have been reported for ascorbic acid, another high value metabolite, whose levels have been shown to increase (Petersen *et al*., 1998) or decrease (Dumas *et al*., 2003) in response to water stress and salinity, respectively. A 60% ascorbic acid increase has been found in tomato fruits exposed at EC_w of 15 dS m^{-1}. Due to the involvement of ascorbic acid in several metabolic processes, its synthesis under stress may also depend on the interaction with other factors such as nitrogen availability (De Pascale *et al*., 2001).

Dry matter, soluble solids and titrable acidity have been reported to increase with salinity, also (Mitchell *et al*., 1991). These are all highly desirable qualities for the processed tomato industry. In addition, exposure to moderate salinity may also contribute to maintain low nitrates levels as a result of competition with Cl^-. The increased concentration of total soluble solids in salinized plants is generally associated to a reduced water content, accumulation of ions and *ex novo* synthesis of organic molecules that in hyperosmotic environments have multiple functions, including osmotic adjustment and sequestration of reactive oxygen species. The increased acidity reported for many vegetables grown in saline environment, including eggplant (Savvas and Lenz, 1996), tomato (Kafkafi *et al*., 1982), melon (Feigin *et al*., 1987) and cucumber (Martinez and Cerdá, 1989) has been associated to the production of organic acids that typically accumulate under stress.

One side-effect of salinization is micronutrient deficiency that can derive from both soil alkalinisation and ions competition (Grattan and Grieve, 1999). Salt stress induced micronutrient deficiency may cause abnormal plant growth and irregular fruit development. Potassium (K), copper (Cu) and zinc (Zn) deficiencies have been reported in tomato exposed to salinity (Maggio *et al*., 2004).

Accumulation of functional molecules and ion partitioning has to be considered also respect to the commercial plant organs. In cauliflower, it was observed a significant accumulation of Na^+ and Cl^- ions in the leaves, whereas the concentration of nitrogen (N), K and P was higher in the heads (De Pascale *et al*., 2005). The head concentration of Na^+ and Cl^- was relatively higher in broccoli compared to cauliflower, indicating that different ion transports and accumulation mechanisms may exist in plants belonging to the same gender, yet characterized by different morphology. This may have important implications in the assessment of stress effects and overall definition of the nutritional profile of commercial products (De Pascale *et al*., 2005). Stress induced ion accumulation and partitioning may explain specific responses between different species. Cauliflowers accumulate more Ca^{2+} than broccoli in response to saline stress. This may protect cauliflower plants from tipburn and premature leaf senescence, which are in contrast relatively frequent in broccoli plants. Similarly, Ca^{2+} deficiencies may cause product quality decay in lettuce, endive and fennel (De Pascale and Barbieri, 1995).

Effects of salt stress on ion uptake and accumulation have been observed for sulphur (S) also. Cauliflower head concentrations of S increase in response to salinity, whereas they do not change in leaves. A moderate increase has also been observed in broccoli (De Pascale *et al*., 2005). Sulphur is an important precursor of glucosinolates and isothiocyanates, whose demonstrated anticarcinogenic activity contributes to the nutritional value of brassica species (Barbieri *et al*., 2008). In some cases, analysis of ion partitioning in different organs may reveal important redistribution mechanisms with significant physiological consequences. In carrots, N, Na^+ and Cl^- concentrations of leaves and roots were doubled within the range of electrical conductivity of the saturated-soil extract (EC^e) between 1.9 and 4.2 dS m^{-1} without any significant distinction between the two organs (De Pascale and Barbieri, 2000). In contrast, Na^+ and Cl^- concentrations of stressed radish plants irrigated with 8.5 mM L-proline increased in hypocotils and decreased in leaves (Maggio *et al*., 2009a). It is not understood if the effect of proline treatment on root/shoot ions distribution can be generalized or it is peculiar to radish plants and/or hypertrophic root systems in general. In the latter case, radish and similar plants could be used as models to understand the dynamics of organ ions partitioning in plants exposed to saline stress. An enlarged (hypertrophic) root system may be functional to preserving aboveground edible parts from salt damages. Genes that regulate root development have been isolated and can be transferred via genetic engineering to test their function in stress tolerance/adaptation (Maggio *et al*., 2001; Morant *et al*., 2010).

A mild salt stress may also improve both lypophilic and hydrophilic antioxidant activities. Exposure to moderate salinity (4.4 dS m^{-1}) can increase up to 40% the concentration of carotenoids in tomato fruits (De Pascale *et al*., 2001). This is mainly due to enhanced lycopene content, whose biosynthesis is activated under stress. However, the response of antioxidants metabolic pathways largely depends on the level of stress exposure and other cultural/environmental factors.

Conclusions

In this short review we attempted to highlight some aspects of crop-salinity interactions, mainly associated to different forms of salinization, which may occur in Mediterranean environments. These may range from over-salinized lands of coastal areas, where profound modifications of the soils physicochemical properties may lead to land abandonment, to balanced agro-ecosystems in which moderate salinization contributes to guarantee high value productions (see tomatoes of Pachino area – Sicily). Additional specificities of Mediterranean areas include: i) greenhouse cultivations, for which modifications of climatic parameters and/or root/substrate interactions (hydroponics) may contribute to cope with saline stress; ii) overlaps with other abiotic stress such as high temperature, photoinhibition, anoxia (in sodic soils), atmospheric pollutants (O_3) and biotic stresses, including pathogen and pest attacks; iii) dynamic interactions between plant development and transitory/permanent soil salinization; iv) exposure to seasonal salinization in irrigated spring/summer crops vs. residual soil salinization in fall-winter non-irrigated crops. All these conditions call for a careful assessment of those physiological mechanisms that may have *functional priorities* to overcome salt stress in specific agricultural conditions. In this respect, major physiological processes that control tolerance levels, namely water/ion homeostasis, hormone regulation and metabolic adjustment, growth control and injury control should be re-examined in specific cultural contexts to i) bring current knowledge to a new level of application and ii) identify novel targets to improve field salinity tolerance. Significant progress in this field can be expected from a closer interaction between molecular engineers and crop physiologists.

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