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REVIEW

Plasma membrane permeability as an indicator of salt tolerance in plants

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Abstract

There is evidence that the plasma membrane (PM) permeability alterations might be involved in plant salt tolerance. This review presents several lines of evidence demonstrating that PM permeability is correlated with salt tolerance in plants. PM injury and hence changes in permeability in salt sensitive plants is brought about by ionic effects as well as oxidative stress induced by salt imposition. It is documented that salinity enhances lipid peroxidation as well as protein oxidative damage, which in turn induces permeability impairment. PM protection, and thus retained permeability, in tolerant plants under salt imposition could be achieved through increasing antioxidative systems and thereby reducing lipid peroxidation and protein oxidative damage of PM. It appears that specific membrane proteins and/or lipids are constitutive or induced under salinity which may contribute to maintenance of membrane structure and function in salt tolerant plant species. Furthermore, protecting agents (*e.g.*, glycinebetaine, proline, polyamines, trehalose, sorbitol, mannitol) accumulated in salt tolerant species/cultivars may also contribute to PM stabilization and protection under salinity. Based on the presented evidence that PM permeability correlates with plant salt tolerance, we suggest that PM permeability is an easy and useful parameter for selection of genotypes of agriculture crops adapted to salt stress.

Additional key words: antioxidants, lipid peroxidation, plasma membrane lipids and proteins, protecting agents, oxidative stress, salinity.

Introduction

Salinity is defined as the presence of excessive concentration of soluble salts in the soil or in the irrigation water that suppresses plant growth and eventually yield. Salt stress has been identified as one of the most serious environmental factors limiting the productivity of crop plants (Qadir *et al*. 2008, Flowers *et al*. 2010).

The deleterious effects of salinity on plant growth are associated with *1*) low osmotic potential of soil solution, *2*) nutritional imbalance (Attia *et al*. 2011), *3*) specific ion effect (Munns and Tester 2008), or *4*) a combination of these factors (Arzani 2008). In addition, there is evidence that salt stress can induce oxidative stress due to generation of reactive oxygen species (ROS), including singlet oxygen, superoxide anion, hydrogen peroxide and hydroxyl radical (Mittler 2002, Gill and Tuteja 2010, Malik *et al.* 2011, Attia *et al.* 2011). ROS attack the cellular macromolecules, such as proteins, nucleic acids and membrane lipids causing their damage.

High substrate salinity is first encountered by the PM of the root cells. The consequences of this are manifested by the alterations in membrane permeability (Mansour *et al*. 1993, Mansour and Stadelmann 1994, Mansour 1997, Ashraf and Ali 2008), membrane lipid composition (Mansour *et al*. 1994, 2002b, Wu *et al*. 1998, 2005, Kerkeb *et al*. 2001, Salama *et al*. 2007), membrane potential (Serrano *et al*. 1999) and activities of membrane bound enzymes (Mansour *et al*. 2003, Qiu *et al*. 2007, Senadheera *et al*. 2009, Cosentino *et al*. 2010). Therefore, several studies suggest that the PM might be a primary site of salt injury (Maas and Nieman 1978, Levitt 1980, Cramer *et al*. 1985, Lauchli 1990, Mansour 1997, Mansour and Salama 2004). In addition, PM permeability has been reported as an effective selection criterion for salt tolerance in various crops (Sairam *et al*. 2002, Flowers and Flowers 2005, Farooq and Azam 2006, Ashraf and Ali 2008, Tuna *et al*. 2009, Collado *et al*. 2010, Munns 2010, Tiwari *et al*. 2010).

The PM allows certain molecules or ions to pass in

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Abbreviations: EC - electrical conductivity; PA - phosphatidic acid; PC - phosphatidylcholine; PE - phosphatidylethanolamine; PEG - polyethyleneglycol; PG - phosphatidylglycerol; PI - phosphatidylinositol; PM - plasma membrane; ROS - reactive oxygen species.

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and out of the cell, while forming a barrier against others. The passage of ions and nonelectrolytes occurs through transport proteins (*i.e.*, channels, carriers) as well as lipid phase of the membrane (Stadelmann and Lee-Stadelmann 1989, Mansour 1997, Wang *et al*. 2008). In the current review, we deal also with nonelectrolyte permeability (*i.e.*, urea, methylurea, ethylurea) that crosses the membrane through its lipid portion and transport proteins (Stadelmann and Lee-Stadelmann 1989, Mansour 1997, Wang *et al*. 2008). The review also deals with electrolyte leakage, as a measure for changes in PM permeability, that is primarily controlled by membrane transport proteins (Serrano *et al*. 1999, Jacobs *et al*. 2011). Changes in nonelectrolyte permeability and electrolyte leakage under saline conditions, therefore, will indicate modifications in the proteins and lipid matrix of the PM. Several investigations indicated that PM permeability was altered markedly in salt sensitive cultivars whereas the effect was minimal in salt tolerant ones under saline conditions (Leopold and Willing 1984, Zongli *et al*. 1987, Mansour *et al*. 1993, Mansour and Stadelmann 1994, Mansour 1997, Ashraf and Ali 2008, Yang *et al*. 2009, Tuna *et al*. 2009). We propose that the PM stability of salt tolerant cultivars is maintained (and hence permeability) *via* inherited or induced membrane protection under salt imposition. The published data supports our previous contention for maintenance of the PM integrity in salt tolerant plants under saline conditions. Firstly, PM integrity was retained in salt tolerant plants under salt stress through sustained lipids and proteins composition (Lauchli 1990, Mansour *et al*. 1994, 2002b, 2003, Mansour 1997, Wu *et al*. 1998, 2005, Kerkeb *et al*. 2001, Mansour and Salama 2004, Salama *et al*. 2007, Amtmann and Beilby 2010, Jacobs *et al*. 2011). Secondly, various protecting agents accumulate and stabilize the PM against salt stress in salt tolerant plant species (Hasegawa *et al*. 2000, Mansour 1995a, 1997, 1998, 2000, Mansour *et al*. 2002a, Garg *et al*. 2002, Chen *et al*. 2007, Cuin and Shabala 2008, Chen and Murata 2011, Ghanti *et al*. 2011). Thirdly, PM lipid peroxidation and protein oxidative alterations were much lower in salt tolerant cultivars relative to salt sensitive ones (Zhu 2001, Alvarez-Pizarro *et al*. 2009, Panda and Khan 2009, Hajlaoui *et al*. 2009, Olias *et al*. 2009, Avery 2011).

This review presents information on the influence of salinity stress (*i.e.*, osmotic, ionic and oxidative stress) on the PM permeability of species/cultivars contrasting in their response to salinity. Mechanisms that are possibly involved in the PM permeability alterations are presented. Strategies underlying PM integrity maintenance in salt tolerant species/cultivars under saline conditions are also included. Evidence that indicates the PM permeability correlation with salt tolerance in plants is clearly documented.

Measurement of the PM permeability

Electrolyte leakage method: Leakage of either organic solutes or ions from a plant tissue (usually leaf discs) subjected to continuous shaking for a specific time period was determined as a measure for changes in PM permeability after salt exposure. The electrical conductivity (EC) of the leaf discs bathing medium (usually deionized water) is then measured. The EC is usually measured initially and after keeping the samples in high or at freezing temperature, and the ratio of the EC measurements represents the membrane stability index or relative membrane permeability (Zongli *et al*. 1987, Sairam *et al*. 2002, Farooq and Azam 2006, Ashraf and Ali 2008, Daneshmand *et al*. 2010, Munns 2010, Tiwari *et al*. 2010). In these studies, the increase in electrolyte leakage, induced by salinity, has been always used to indicate increased PM permeability. It is important to mention that ions leak out from the leaf discs essentially through membrane transport proteins (*i.e.* channels and carriers) and also through membrane lipid portion. It is, therefore, expected that increased PM permeability induced by salt stress reflects alterations in both membrane components (proteins and lipids). In other studies, leakage of organic solutes into the external solution was determined by measuring the absorbance of the bathing medium (Poovaiah and Leopold 1976, Leopold and Willing 1984). Accumulation of radioactive calcium in shoot and root of wheat genotypes was also used to indicate changes in PM permeability (Dwivedi *et al*. 1981).

Although in the previous works leakage of solute was employed as an indicator of membrane lesions, the exact mechanism of membrane injury has not been clearly defined. A more precise characterization of the nature of membrane injury, however, is required to understand the involvement of the cell membrane in plant salt tolerance. Furthermore, leakage from leaf discs exposed to salt indicates only overall permeability and may mask possible great differences between salt treatment and controls in individual tissues and cell types (Mansour 1997). However, using the electrolyte leakage as a measure to indicate the PM injury and hence genotype differences under salt stress is still feasible and has been reported to be an efficient screening technique for salt tolerance (Munns 2010).

Plasmometric method: The PM permeability can be measured under various conditions by a technique developed by Stadelmann and Lee-Stadelmann (1989). Practically, the cells of plant sections are plasmolyzed stepwise in a series of glucose concentrations (*e.g.* 0.4, 0.6 and 0.8 mM). The tissue is left for 15 min in the first two concentrations and 30 - 45 min in the last solution to reach osmotic equilibrium. The tissues are then transferred onto a perfusion chamber along with a droplet of the last solution. Next, the perfusion chamber is covered by a cover slip sealed with vaseline and mounted on a microscope stage. The plasmolyticum in the perfusion chamber is then exchanged with an equiosmolar solution of urea. The protoplasts will deplasmolyze with the entry of the urea and water into the vacuole. The increase in the protoplast size is measured at time intervals by a micrometer. The length of the deplasmolyzing protoplast is plotted against time and the permeability coefficient is calculated for each individual cell using the formula of Stadelmann and Lee-Stadelmann (1989).

Response of PM permeability to salinity stress in plants contrasting in salt tolerance

The alterations in PM permeability varied significantly between species and cultivars of different salt tolerance. PM permeability to nonelectrolytes was increased and that of water was decreased markedly in salt sensitive cultivars of wheat and barley upon salt treatment (Mansour *et al.* 1993, Mansour and Stadelmann 1994, Mansour 1995b, 1997, Mansour and Salama 1996, 2004). Changes in PM permeability of salt tolerant cultivars under salt stress were, however, always marginal. Additionally, bathing of onion (salt sensitive) bulb epidermal cells in 150 mM NaCl solution for 4 h increased the PM permeability of these cells (Mansour 1995a, 1998). It is interesting to mention that agents (glycinebetaine, proline, calcium) that protect PM against salinity stress bring the Na^+-increased PM permeability coefficient in salt sensitive cultivars back to the control values (Mansour 1995a, 1997, 1998), indicating that changes in PM permeability is a sensitive probe for membrane alterations. PM permeability alterations have been observed in salt sensitive species without reduced growth or severe chlorosis, again suggesting that the PM permeability is a sensitive test for salt stress and tolerance (Mansour and Salama 2004). Moreover, toxic lesions (*i.e.* swollen protoplasm and cell mortality) produced from the injured PM induced by salt stress were more pronounced in salt sensitive plants (Mansour *et al.* 1993, Mansour 1997, Mansour and Salama 2004).

When electrolyte leakage was used to measure PM permeability, a close relation between the PM permeability and salt tolerance was reported in different plant species (Dwivedi *et al.* 1981, Leopold and Willing 1984, Zongli *et al.* 1987, Tuna *et al.* 2009, Yang *et al.* 2009, Daneshmand *et al.* 2010, Kholova *et al.* 2010). Other studies, used tissue leakage as an indicator of PM permeability, also support the more susceptibility of the PM of salt sensitive plants to salinity (Farooq and Azam 2006, Ashraf and Ali 2008, Hajlaoui *et al.* 2009, Tuna *et al.* 2009, Tiwari *et al.* 2010, Ben Amor *et al.* 2010). On the other hand, maintenance of PM permeability was related to salt tolerance in the studied plant species.

High concentration of ions in the soil lowers the water potential of soil solution. To test the effect of osmotic potential on the PM permeability, iso-osmotic concentration of non-permeating solute (usually polyethylene glycol, PEG, or mannitol) and NaCl were used. When soybean leaf discs were exposed to 400 mM sorbitol to induce osmotic stress (osmotically equivalent to 200 mM NaCl), the leakage of solutes was very low compared with that induced by NaCl (Leopold and Willing 1984). PEG (10 000) at 219 mM (equivalent to 100 mM NaCl) added to the nutrient solution for 5 d resulted in no significant change in PM permeability of cells from either sensitive or tolerant cultivars of barley (Mansour *et al.* 1993). Moreover, osmotic stress induced by 328 mM mannitol (equivalent to 150 mM NaCl) had no effect on the PM permeability of *Allium cepa* epidermal cells (Mansour 1995a). In support to the absence of osmotic stress impact on PM permeability is the evidence that NaCl-induced rupture of PM during permeability measurements was not observed under osmotic stress induced by non-permeating compounds (Mansour *et al.* 1993, Mansour 1995a). Osmotic stress brought about by salinity was reported not to be the limiting factor for plant growth reduction at high salinity, but rather salt toxicity (Termaat *et al.* 1985, Munns and Termaat 1986, Shalata and Neumann 2001, Roshandel and Flowers 2009). It can be, therefore, concluded that the osmotic component of salinity stress does not seem to be a major factor causing membrane injury and subsequent alteration of PM permeability under saline conditions.

It is evident that salt stress induces production of ROS, which cause injury to cellular proteins, nucleic acids and membranes (Mittler 2002, Ashraf 2009, Gill and Tuteja 2010, Attia *et al.* 2011, Malik *et al.* 2011). ROS attack membrane lipids and proteins resulting in lipid peroxidation and oxidative damage of proteins, which impairs membrane structure and hence permeability (Vercesi *et al.* 1997, Panda and Khan 2009, Kholova *et al.* 2009, 2010, Hajlaoui *et al.* 2009, Tarchoune *et al.* 2010, Ben Amor *et al.* 2010, Gill and Tuteja 2010, Avery 2011). One can, therefore, expect that salt tolerant plant species increase antioxidant systems and thereby decrease membrane lipid peroxidation and oxidative alterations of proteins, hence protecting the membrane structure and function. Previous published data is in agreement with this hypothesis. Several studies addressed this issue by measuring membrane lipid peroxidation, PM permeability, and antioxidative defense systems in absence and presence of salt imposition (Khan and Panda 2008, Aghaei *et al.* 2009, Alvarez-Pizarro *et al.* 2009, Hajlaoui *et al.* 2009, Kholova *et al.* 2009, 2010, Panda and Khan 2009, Yang *et al.* 2009, Ben Amor *et al.* 2010, Collado *et al.* 2010, Tarchoune *et al.* 2010, Attia *et al.* 2011, Malik *et al.* 2011). These studies indicated that salt tolerance was always related to minimized membrane lipid peroxidation. In addition, Ashraf and Ali (2008) demonstrated that retained PM permeability and increased activities of antioxidant enzymes were very effective in discriminating the canola cultivars for salt tolerance.

PM damage was lower in transgenic tobacco (Gao *et al.* 2006) and transgenic alfalfa (Bao *et al.* 2009) overexpressing the H^+-pyrophosphatase (H^+-PPase) than in the respective wild type under salt stress. Moreover, overexpression of Yes-associated protein 1 gene (*YAP1*) increased activities of antioxidant enzymes and improved the PM permeability in transgenic *Arabidopsis* under saline conditions (Zhao *et al.* 2009). In these studies, not only retained PM permeability due to lower membrane lipid peroxidation but also lower Na^+ content in the cytoplasm in the transgenic plants, contributed to improved salt tolerance.

We thus conclude that salinity-induced oxidative stress (*i.e.* oxidative damage of membrane proteins and lipid peroxidation) contributes to the increased PM permeability in salt sensitive plant species, whereas the improved PM integrity and thus maintained permeability in salt resistant species is a result of reduced oxidative damage.

Mechanisms of salinity-induced permeability alterations

Biomembranes are composed of lipids and proteins and it is documented that membrane lipids are responsible for determining major biological properties of the membranes (Uitert *et al.* 2010). In addition, membrane proteins play a crucial role in regulating ion transport across the membrane (Amtmann and Beilby 2010, Sade *et al.* 2010, Jacobs *et al.* 2011). Membrane proteins may also assist in maintaining bilayer structure (Bishop 1983). Passive permeability is mainly controlled by membrane lipid portion as well as membrane transport proteins (Stadelmann and Lee-Stadelmann 1989, Mansour 1997, Mansour *et al.* 2003, Wang *et al.* 2008). The changes in PM permeability thus reflect changes in the membrane lipids and proteins structure/composition and lipid-protein interaction (McElhaney *et al.* 1973, Simon 1974, Van Zoelen *et al.* 1978, Jackson and John 1980, Carruthers and Melchoir 1983, Zwiazek and Shay 1988, Stadelmann and Lee-Stadelmann 1989, Magin *et al.* 1990, Mansour 1997, Mansour and Salama 2004, Collado *et al.* 2010, Zamani *et al.* 2010).

Membrane lipids: Alterations in PM permeability under salinity have been ascribed to changes in membrane lipids (Bishop 1983, Stadelmann and Lee-Stadelmann 1989, Mansour *et al.* 1993, Mansour 1995b, Wassall and Stillwell 2009). PM lipid composition have been altered in different plant species upon salt imposition (Douglas and Walker 1984, Douglas, 1985, Brown and DuPont, 1989, Blits and Gallagher 1990, Mansour *et al.* 1994, 2002b, Wu *et al.* 1998, 2005, Kerkeb *et al.* 2001, Salama *et al.* 2007, Bargmann *et al.* 2009, Zamani *et al.* 2010). The reduced changes in PM lipids induced by salinity are expected to promote maintenance of membrane integrity and cellular homeostasis in salt tolerant species. Such membrane adaptation might be, however, lacking in sensitive plants.

Sterols: PM from halophytes was found to be constitutively rich in sterols and maintenance or elevation in sterol/phospholipids ratio was also observed under saline conditions (Blits and Gallagher 1990, Wu *et al.* 1998, 2005, Alvarez-Pizarro *et al.* 2009). High free sterols in the PM of citrus genotypes with high Cl^- exclusion and in the PM of sugar beet roots have been reported (Douglas and Walker 1984, Yahya *et al.* 1995). Sterol/phospholipids ratio was also increased in salt tolerant maize cultivar (Salama *et al.* 2007) and tomato (Kerkeb *et al.* 2001). Increased free sterols and sterol/phospholipids ratio of PM have been reported to modulate membrane fluidity and in turn permeability (Thompson *et al.* 1983, Shinitzky 1984, Russell 1989, Kerkeb *et al.* 2001, Khan *et al.* 2009). Moreover, Bishop (1983) indicated that maintenance of optimum membrane fluidity is the overriding criterion for successful membrane function. In addition, more planar free sterols (cholesterol, campesterol) are more efficient than less planar free sterols (stigmasterol, sitosterol) in regulating membrane stability and hence permeability (Douglas and Walker 1984, Kuiper 1984, Mansour *et al.* 1994). The results reported so far in this respect are variable and species specific. Salinity decreases the amount of more planar free sterols in halophyte *Spartina patens* (Wu *et al.* 1998), in salt tolerant tomato calli (Kerkeb *et al.* 2001), and in salt sensitive wheat (Mansour *et al.* 2002b), whereas it increases these sterols in salt sensitive wheat (Mansour *et al.* 1994), in tolerant sugar beet (Yahya *et al.* 1995), in sensitive tomato (Kerkeb *et al.* 2001), and in sensitive and tolerant genotypes of soybean (Zenoff *et al.* 1994). Despite these contrasting data, the role of membrane sterols in modulating PM permeability cannot be excluded (Bargmann *et al.* 2009, Wassall and Stillwell 2009).

Phospholipids: PM phospholipid alterations are reported in various plant species under salinity (Mansour *et al.* 1994, 2002b, Douglas and Walker 1984, Hiryama and Mihara 1987, Yahya *et al.* 1995, Kerkeb *et al.* 2001, Wu *et al.* 1998, 2005, Salama *et al.* 2007, Zamani *et al.* 2010). The change in PM phospholipid classes and its impact on membrane permeability could be explained by the fact that phosphatidylglycerol (PG) and phosphatidylcholine (PC) tend to form bilayer structure, whereas phosphatidylethanolamine (PE), phosphatidic acid (PA) and phosphatidylinositol (PI) are nonbilayer forming lipids (Cullis and De Kruijff 1979, Quinn 1983, Gagne *et al.* 1985). Nonlamellar domain in the membrane renders high permeability (Bishop 1983, Russell 1989). Moreover, the cell permeability can be significantly altered by the conversion of part or all of the phospholipids from lamellar to hexagonal orientation (Bishop 1983, Thompson *et al.* 1983). Increased abundance of PE and PI in the PM of salt sensitive plant species under salt stress was reported (Norberg and Liljenberg 1991, Mansour *et al.* 1994, 2002b, Racagni *et al.* 2003, Salama *et al.* 2007) which also explains increased permeability in these salt sensitive species.

Fatty acids: One common influence of salinity on PM fatty acids is the increasing degree of saturation of membrane fatty acids (Mansour *et al.* 1994, 2002b, Surjus and Durand 1996, Wu *et al.* 1998, 2005, Kerkeb *et al.* 2001, Salama *et al.* 2007). Subsequently, the unsaturated/saturated fatty acid ratio decreases. Increasing membrane fatty acid saturation and decreasing unsaturated/saturated ratio may induce a phase separation in the PM, which also changes the membrane fluidity and permeability (Bishop 1983, Kuiper 1984, Senaratna *et al.* 1984, Rochester *et al.* 1987, Russell 1989). Root extracts from maize salt tolerant cultivar showed lower proportion of saturated fatty acids compared with salt sensitive one (Hajlaoui *et al.* 2009). Based on the previous evidence, we believe that increased fatty acid saturation correlates with salt sensitivity. However, changes in fatty acid saturation are found in both salt sensitive and tolerant species/cultivars despite the different response in PM permeability. This might be explained by the fact that some changes (*e.g.* increased saturated fatty acids content) in the PM of salt tolerant species are likely counterbalanced by other changes (*e.g.* increased PG or PC) so that the PM integrity is maintained (Mansour *et al.* 1994, Mansour and Salama 2004, Salama *et al.* 2007).

Membrane proteins: Salinity-induced changes in the membrane transport proteins can also affect protein-lipid interaction which finally can alter PM permeability (Simon 1974). It is possible that membrane transport proteins first undergo conformational changes, which in turn, disturb specific molecular interactions between lipids and proteins and eventually affects membrane permeability (Simon 1974, Mansour 1997). Additionally, changes in the configuration of membrane proteins could also lead to different spacing of the phospholipids, because of the polar interactions between both types of molecules (Levitt 1980, Russell 1989). This can further affect PM permeability. Moreover, salt-induced changes in lipid microenvironment around transport proteins affect their kinetic properties and the efficiency of the transport systems (Mansour *et al.* 2003, Amtmann and Beilby 2010). Impaired functions of transport proteins (reflected in increased PM permeability) will increase Na^+ absorption under salinity. It is reasonable, therefore, to conclude that membrane protein alterations under salinity might be enhanced in salt sensitive cultivar/ species, but not so much in salt tolerant ones (Olias *et al.* 2009, Amtmann and Beilby 2010, Sade *et al.* 2010, Jacobs *et al.* 2011).

Really, different alterations in the PM proteins were found in plant species/genotypes differing in salt sensitivity under saline conditions (Singh *et al.* 1987, Hurkman *et al.* 1988, Kononowicz *et al.* 1994, Mansour *et al.* 2000, 2002b, Salama *et al.* 2007, Zamani *et al.* 2010). Furthermore, qualitative and quantitative differences in the PM proteins have been found in salt sensitive and tolerant plants after salt treatment (Mansour *et al.* 2002b, Goncalo *et al.* 2003, Salama *et al.* 2007, Zamani *et al.* 2010). The amount of PM H^+-ATPase was increased in salt tolerant wheat and rice whereas it decreased in sensitive ones upon salt imposition (Zhang *et al.* 1999, Yang *et al.* 2009). In addition, expression of V-ATPase in salt tolerant rice was increased (Abdul Kader *et al.* 2006). In response to salinity, PM protein elevation and depression were found in salt sensitive and resistant wheat (Salama *et al.* 2007) and tomato (Kerkeb *et al.* 2001). However, protein pattern of PM from wheat sensitive and tolerant roots (Mansour *et al.* 1998, 2000) and from sugar beet roots (Yahya *et al.* 1995) did not change under salinity imposition. Salt-induced 29 kDa protein (osmotin) in tolerant genotypes has a protective function (Singh *et al.* 1987, Hurkman *et al.* 1988, Kononowicz *et al.* 1994, Salama *et al.* 2007). It is most likely that the alterations in the PM proteins of salt tolerant plants under salt stress are usually in a direction to maintain their stability and hence PM permeability. On the other hand, the salinity-induced changes in the PM proteins of salt sensitive plants might disrupt their PM structure resulting in increased permeability. Transgenic plants overexpressing pepper pathogen-induced membrane protein 1 (CaMIMP1), exhibited enhanced tolerance to environmental stresses including NaCl (Hong and Hawang 2009). In addition, Very and Sentanac (2009) reported that PM-associated proteins might be involved in plant homeostasis and stress tolerance. Salt-induced new proteins in the PM were also suggested to be associated with salt tolerance in different plants (Singh *et al.* 1987, Hurkman *et al.* 1988, Sung *et al.* 1996, Blumwald 2000, Mansour and Salama 2004, Salama *et al.* 2007, Zamani *et al.* 2010).

Oxidative stress: Salt stress induces production of ROS, which cause injury to cellular proteins, nucleic acids, and membranes. Transgenic plants that have lower lipid peroxidation showed improved PM permeability and enhanced salt resistance under salt imposition (Chinnusamy *et al.* 2005, Gao *et al.* 2006, Bao *et al.* 2009, Zhao *et al.* 2009). Furthermore, the increase in PM permeability induced by lipid peroxidation was always greater in salt sensitive cultivars (Ashraf and Ali 2008, Alvarez-Pizarro *et al.* 2009, Ashraf 2009, Panda and Khan 2009, Hajlaoui *et al.* 2009, Kholova *et al.* 2009, Yang *et al.* 2009, Collado *et al.* 2010) which also confirms a relation between increased PM permeability and lipid peroxidation. Similarly, high membrane stability was related with no increase in PM permeability and lipid peroxidation under high temperature (Collado *et al.* 2010, Dias *et al.* 2010). We can, therefore, infer that salt tolerant plant species combat oxidative stress by increasing the production of antioxidant systems and thereby minimizing lipid peroxidation, the mechanism that ensured membrane protection and hence retained PM permeability. However, salt sensitive cultivars have a low capacity for generation of antioxidants under salinity, and therefore, the PM permeability is impaired.

The mechanism by which lipid peroxidation increases PM permeability might be that lipid peroxidation products are responsible for ordering phospholipids into gel phase which destabilizes the membrane structure (Thompson *et al.* 1983, Russell 1989). In addition, oxidative damage of membrane proteins induces destabilization of their configuration (Gill and Tuteja 2010). This also further contributes to increased PM permeability.

Other factors: Various compounds (including glycine betaine, proline, polyamines, trehalose, sorbitol and mannitol) accumulate in salt tolerant plants (Hanson and Grumet 1985, Mansour 2000, Cuin and Shabala 2008, Chen and Murata 2011, Ghanti *et al.* 2011). It has been reported that these compounds protect the PM under salinity stress (Mansour 1997, 1998, 2000, Cuin and Shabala 2008, Chen and Murata 2011).

Glycinebetaine and proline proved to be efficient protectants of the PM (Mansour 1998, Ashraf and Foolad 2007, Ghanti *et al.* 2011). Glycinebetaine was superior to proline in onion epidermal cells (Mansour 1998). Elevated proline content in transgenic chickpea plants protected PM (resulted in reduced electrolyte leakage) and hence alleviated salt stress (Ghanti *et al.* 2011). High accumulation of glycinebetaine and proline under salt stress was found in salt tolerant plants whereas salt sensitive ones exhibited a low accumulation capacity for both solutes (Mansour 2000, Ashraf and Foolad 2007, Cuin and Shabala 2008). Similarly, ascorbic acid mitigated NaCl-induced PM permeability alterations in onion epidermal cells (Salama 2009). Moreover, exogenous application of ascorbic acid lowered lipid peroxidation induced by salinity stress and hence protected PM of tomato seedlings (Shalata and Neumann 2001).

Also accumulation of polyamines is related with salt tolerance in plants (Bouchereau *et al.* 1999, Mansour 2000, Takahashi and Kakehi 2010). Protection of the PM by polyamines resulting in permeability maintenance in different plant species under salt stress was documented (Mansour and Al-Mutawa 1999, Mansour 2000, Takahashi and Kakehi 2010).

Calcium also plays an important role in stabilizing cell membranes and hence improves plant salt tolerance (Cramer *et al.* 1985, Kent and Lauchli 1985, Lauchli 1990, Mansour 1995a, Hirshi 2004). Cell membrane alterations induced by NaCl in onion bulb epidermal cells were alleviated by addition of Ca^{2+} (Mansour 1995a). Furthermore, salt tolerance in barley cultivars was attributed to high amount of Ca^{2+} binding to cell membrane under salt stress (Bittisnich *et al.* 1989). Therefore, displacement of Ca^{2+} from its binding sites in the cell membranes had great impact on membrane stability and hence salt tolerance (Cramer *et al.* 1985, Lauchli 1990).

Conclusions and future prospects

The data discussed above show that PM permeability is a reliable physiological measure for salt tolerance, and therefore, is recommended as a good selection criterion for breeding. It is also evident that PM permeability is a sensitive indicator for changes in membrane lipids and proteins. PM permeability in salt sensitive cultivars, species, and lines is more impaired by salt imposition than in salt tolerant ones. Specific ion effects and oxidative stress caused by salinity are most likely the main factors induced PM permeability impairment whereas decrease in osmotic potential is less important. Altered lipids and proteins of the PM are the main mechanisms that bring about permeability changes under saline conditions. Production of antioxidants and membrane protecting compounds help salt tolerant plant species to withstand salt exposure. It is reasonable to believe that specific membrane lipid classes and sustainable transport proteins are constitutive or induced under saline conditions which might contribute to salt tolerance. The importance of the PM component changes under salinity stress relies on the fact that these changes may eventually disrupt the PM stability and thus accelerate efflux of intracellular solutes and influx of Na^+ from the rooting medium. Furthermore, PM transport systems regulate ion homeostasis either through exclusion or absorption of ions under salt imposition (Mansour *et al.* 2003, Qiu *et al.* 2007, Senadheera *et al.* 2009, Cosentino *et al.* 2010). More detailed studies are necessary for a full understanding of the significance of the PM lipids and proteins at the molecular species level in salt tolerance.

There is an evidence indicating that exposure to salinity activates a gene or a set of genes in various plant species (Winicov 1998, Hu *et al.* 2010, Munns 2010). Some of these genes might encode enzymes involved in membrane component alterations and hence affect ion homeostasis by stabilizing the PM under salinity. Identification of genes involved in membrane-component alterations, that might correlate with salt tolerance, should ultimately enhance our capacity to breed crops with improved salt tolerance.

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