437

Physiological responses of plants to salinity: A review

K. M. Volkmar[1], Y. Hu[2], and H. Steppuhn[2]

[1]*Agriculture and Agri-food Canada, Brandon Research Centre, PO Box 1000A, RR#3, Brandon, Manitoba, Canada R7A 5Y3; and* [2]*Semi-arid Prairie Agriculture Research Centre, Agriculture and Agri-food Canada, PO Box 1030, Swift Current, Saskatchewan, Canada S9H 3X2.* *Received 10 February 1997, accepted 29 August 1997.*

Volkmar, K. M., Hu, Y. and Steppuhn, H. 1998. **Physiological responses of plants to salinity: A review.** Can. J. Plant Sci. 78: 19–27. Root-zone salinization presents a challenge to plant productivity that is effectively countered by salt-tolerant halophytic plants, but unfortunately, much less successfully by major crop plants. The way in which salt affects plant metabolism is reviewed. Cellular events triggered by salinity, namely salt compartmentation, osmotic adjustment and cell wall hardening are connected to the whole plant responses, namely leaf necrosis, altered phenology and ultimately plant death. The roles of ion exclusion and K/Na discrimination in mediating crop response to salt appear to be central to the tolerance response, but they are by no means essential. The processes involved in regulating ion uptake at the membrane level are considered. Recent work elucidating the interaction between calcium and salinity tolerance is reviewed.

Key words: Cell growth, cell turgor, ion regulation, K^+/Na^+ discrimination, osmotic adjustment, salt tolerance

Volkmar, K. M., Hu, Y. et Steppuhn, H. 1998. **Réponse physiologique des plantes à la salinité: Mise au point bibliographique.** Can. J. Plant Sci. 78: 19–27. La salinisation de la rhizosphère est un obstacle à la productivité végétale, qui est exploité avec succès par les plantes halophytes (tolérantes au sel), mais qui est beaucoup plus difficile à surmonter pour les principales espèces cultivées. Les auteurs présentent une mise au point bibliographique des effets des sels sur le métabolisme végétal. Les phénomèmes cellulaires déclenchés par la salinité, notamment la compartimentation des sels, les adaptations osmotiques, le durcissement des parois cellulaires sont reliés aux réactions de la plante, nécrose foliaire, perturbation phénologique et finalement la mort. L'exclusion et la discrimination K/Na dans la médiation des réponses de la plante semblent être au centre des réactions de tolérance, encore qu'elles ne soient en aucun point essentielles. Les auteurs analysent les mécanismes impliqués dans la régulation de l'absorption ionique au niveau membranaire. Ils passent également en revue les travaux récents éclairant l'interaction entre le calcium et la tolérance à la salinité.

Mots clés: Croissance cellulaire, turgesgence de la cellule, régulation ionique, discrimination K^+/Na^+, adaptation osmotique, tolérance au sel

A generalized model of plant response to salt stress will be described, relating the whole-plant manifestations of root-zone salinity to initial responses to soil salinity at the cellular level.

PRINCIPLES

There is a continuous spectrum of plant tolerance to saline rooting media, ranging from very sensitive glycophytes showing the effects of salt at concentrations of less than 1/10 sea water (50 mol m^{-3}), to halophytes, that complete their life cycles at 500 mol m^{-3} (Flowers et al. 1986; Ungar 1991). The halophyte, *Suaeda maritima*, for example, exhibits a growth optimum of around 200 mol m^{-3} and is able to tolerate root zone salinity levels up to 1000 mol m^{-3} (Clipson et al. 1985). Unfortunately, the major crops are almost universally non-halophytic. For example, bean yield is inhibited almost entirely at 50 mol m^{-3} (Maas 1987).

In the vascular plants that form the bulk of the agricultural crops, water-based soil solutions surrounding their roots become part of the plant's delicately-balanced aqueous environment. Water and selected solutes move from the soil into the plant in response to osmotic potentials existing on opposite sides of root membranes, i.e., down energy gradients. Plants that grow on saline soils are confronted with soil solutions exhibiting diverse ionic compositions and a wide range in the concentrations of dissolved salts. Concentrations fluctuate because of changes in water source, drainage, evapotranspiration, solute availability, hydrostatic pressures, etc. Ionic constituents include varying proportions of Na^+, Ca^{++}, Mg^{++}, K^+, SO_4^-, CO_3, HCO_3^-, and Cl^- and other ions.

The stresses imposed by salinity relate to ion composition and to ion concentration within the plants. When dissolved salt concentrations in soil solutions increase, water energy gradients decrease, making it more difficult for water and nutrients to move through root membranes and into the plant. The rate of water and solute uptake slows, but does not cease. With time, the solute-rich soil water increases ionic concentrations within the plant's aqueous transportation stream. This osmotic effect, encountered at the root membrane, applies at all the plant's internal membranes served by its conductive tissue.

In addition to the osmotic effect of concentrated solutes, there are ionic effects that arise from the specific composition of the solute flowing through plant tissue. Internal excesses of particular ions may cause membrane damage, interfere with solute balances, or cause shifts in nutrient concentrations. Some specific symptoms of plant damage may be recognized especially in the leaves: color change, tip-burn, marginal necrosis, succulence, etc.

The leaves of glycophytic plants cannot retain high levels of salt without injury, and are often not challenged by lethal salt concentrations in their natural habitats. By comparison, halophytes preferentially accumulate salt in the leaves, and these are used to balance the osmotic potential of the salts outside the plant (Flowers et al. 1986). This difference between halophytes and glycophytes in their contrasting adaptive strategies is significant. Halophytes could not survive in saline environments without using the concentrated salts of the soils in which they are growing as a balancing osmoticant. Lacking this adaptive mechanism, glycophytes are unable to survive in environments in which halophytes thrive. Whether glycophyte or halophyte, however, the biosynthetic processes fundamental to plant metabolism, e.g., photosynthesis and respiration, are equally sensitive to salts (Greenway and Osmond 1972). Resilience to salt accumulation resides in the ability of the plant to restrict salt encroachment into the cytoplasm so that enzymic processes are not adversely affected. This must be accomplished while striking a favourable balance between the water potential of the soil solution and that of the plant, to facilitate water entry.

The rate at which salt accumulates in the leaf depends on the ability of living cells along the pathway to the leaf to screen the salt from the cell sap before it reaches the leaf. While it might be assumed that halophytes and glycophytes differ primarily in the salt retention characteristics of their respective root systems, the conclusion in this review is that the fundamental distinction to be made is in their differing abilities to compartmentalize salt in their leaves.

In the following section, we briefly outline the series of events that lead to eventual plant death following exposure to lethal levels of salt in solution. This account is a synthesis of opinions and reviews published over the past 20 yr. For a more detailed and documented account of the concepts developed here the reader is directed to earlier reviews (Flowers et al. 1977; Munns et al. 1983; Yeo and Flowers 1986; Munns 1994). It should be emphasized that parts of the puzzle relating to processes that occur during plant salinization remain incomplete.

THE FATE OF SALT AFFECTED PLANTS

The topic of this section is the sequence of events that gives rise to cell and ultimately plant death. Emphasis is placed on events occurring in the shoots. This is not to disregard the important contributions of salt exclusion and ion discrimination mechanisms operating in the root system that regulate the initial entry of salt ions into the plant, and which for some species appears to determine their salt tolerance (Bernstein and Hayward 1958; Schachtmann and Munns 1992). This topic will be addressed in more detail in later sections. Even for plants that survive in saline soils by minimizing salt ion entry, no matter how efficient the exclusion process, there is a solute concentration which will exceed the root systems' capacity to entirely exclude the ion. At that point salt ions will begin to accumulate in the shoot.

Salinity Effects on Cell Growth

Early Response

Once saline solutes reach the leaf there are really only two mechanisms to exclude them from the cytoplasm. Salt ions can build up in the apoplast, the network of spaces between the cells, or be isolated within the vacuole, a membrane encapsulated vessel within the cell. Accumulation of salt in the apoplast would gradually increase the osmotic gradient between the inside and outside of the cell. To achieve a thermodynamic equilibrium, water inside the cell would move outward into the intercellular spaces, leading to progressive cellular dehydration and, eventually, cell death. In any case, apparent contiguity of the transpiration stream with the cytoplasm (Canny 1995) may make it impossible for salt ions to discharge from the xylem stream into the apoplast. It is therefore most probable that once saline solutes reach the shoot they are partitioned into the cell vacuole. The vacuole comprises the bulk of the total cell volume, and is therefore well-suited for solute compartmentation. By comparison, the symplastic volume, i.e., the cytoplasm, can represent as little as 1% of the cell's volume (Winter et al. 1993), and is therefore potentially sensitive to even slight changes in rate of saline transport into the cell. The sensitivity of the cytoplasmic-based metabolic machinery to saline conditions (Greenway and Osmond 1972) would seem to preclude the occurrence of concentrated inorganic solutes in that compartment. Nonetheless, the technical constraints of sampling solute composition and concentration of the cytoplasm hampers a definitive understanding of the role of the cytoplasm in salt storage. On the other hand, the significance of salt storage capacity of the leaf in sustaining high rates if salt ion transport has been shown (Yeo and Flowers 1986), thus supporting the importance of salt storage capacity of the vacuole in plants exposed to saline conditions.

Salt ions must pass across the plasma membrane, the membrane separating the inside and outside of the cell, into the cytoplasm, before entering the vacuole. The rate of solute delivery across the plasma membrane must not exceed the rate of deposition into the vacuole to minimize the risk of salt damage. Furthermore, because an inability of the cell to compartmentalize the salt ions at a rate comparable to salt delivery would result in their leakage into the cytoplasm and the apoplastic space outside of the cell, the movement of salt ions into the vacuole must match the rate of export of salt from the root to the leaves. This depends upon the ion storage capacity of the root, and the salt concentration in the soil solution. In summary, plant adaptation to salt requires that the vacuolar compartmentation capacity of the cell keeps pace with the rate of delivery of salt ions from the xylem to the leaf.

Cell Growth

Leaf cell growth is sensitive to saline solutes even when export and compartmentalization processes are functioning optimally (McCree 1986). This is due, in part, to an expenditure of energy associated with maintaining an ion gradient favourable for ion compartmentation, as well as an energy cost associated with the synthesis of organic solutes deployed in the comparatively salt-free cytoplasm to balance the osmotic potential of the salt-enriched vacuole. Thus loading of salt within the vacuole will cost the cell energy that could otherwise be used to power biosynthetic processes.

Saline solutions also affect cell growth directly although the precise mechanism by which this occurs remains unclear. According to the biophysical model of cell elongation (Lockhart 1965; Cosgrove 1986), the rate of cell elongation (r) is regulated or controlled by alterations in any of several parameters: cell wall extensibility (ϕ), turgor pressure (P), and yield threshold (Y). Yield threshold (Y) refers to the value of turgor pressure below which no irreversible cell wall extension occurs. ϕ and Y are both cell wall characteristics. This relationship among the parameters may be expressed as:

$r = \phi (P - Y)$ (Lockhart 1965).

From the equation, the limitation of growth by salinity could be due to either a decrease in ϕ and P, an increase in Y, or all of these factors. Because increased salt concentration lowers the osmotic potential of the soil solution, a prevailing notion is that root zone salinity affects growth by lowering cell turgor. Sudden decreases in turgor pressure changes are undoubtedly responsible for the inhibition of growth induced by rapid increase in external solute concentrations.

However, this lowering of cell turgor does not appear to be the cause of the prolonged decrease in leaf elongation rate characteristic of plants growing for long periods in saline solutions. A number of studies have reported decreased leaf growth without any change in cell turgor pressure (Lloyd et al. 1987; Myers et al. 1990; Arif and Tomos 1993) suggesting that the slower growth of salt-stressed plants over longer periods may be attributable to something other than reduced cell turgor. Leaf growth rate of salinized plants was not increased when leaf turgor was artificially raised by pressurizing the root system (Munns 1994; Munns and Termaat 1986). They have suggested that saline salts induce the roots to send a growth regulator-like chemical signal to the shoot that leads to shoot growth inhibition. They related the induction of the signal to a salt-induced decrease in water potential, not to the salt ions themselves.

Others have explored the possibility that salinity reduces cell growth by increasing the yield threshold (Y) or decreasing cell wall extensibility (ϕ). A decrease in ϕ has been reported for both maize roots (Neumann et al. 1994) and leaves (Cramer and Bowman 1991; Neumann 1993) under a long-term salt stress. Several reports have suggested that Y of growing root and leaf tissues may increase in response to salinity stress (Pritchard et al. 1991; Cramer and Bowman 1991; Neumann et al. 1994). Similar observations were made by Newmann et al. (1994) who reported on the growth inhibition of maize root cells in response to 100 mol m^{-3} NaCl.

The capacity of plant leaves to accommodate the export of salt from the root is closely linked to growth rate. New, expanding cells provide a continually replenishing storage reservoir for the vacuolar compartmentalization of salt from the root. In this sense, growth itself represents a means by which the plant can regulate the concentration of salts in the cytoplasm. When cell expansion rate is directly impaired by root-zone salinization, the plant's capacity to accommodate the delivery of salt to the shoot is impaired. The tentative equilibrium established between root export of salt and leaf compartmentalization is disturbed, placing greater pressure on the salt sequestration capacity of the vacuole.

Thus, even though the rate of export of salt ions to the shoot may not change, at some stage during continuous exposure of salt to the plant, the rate of export from the root will exceed the rate of compartmentalization. If this occurs salt ions will accumulate outside the vacuole, either in the cytoplasm or in the intercellular spaces outside the cell. As already mentioned, either option can have disastrous consequences for cell function. In the former case, the cell succumbs directly to ion toxicity. In the latter case, cell expansion will cease entirely, because the driving force for cell expansion, turgor pressure, will have dropped below that of the yield threshold of the cell wall. The loss of water from the cell further concentrates cell solutes to a level where cell metabolism is irreversibly affected.

Whole-plant Response to Salt

The effect of salt on tissue and organ development is reflected in altered patterns of plant growth and development. Continuous exposure to elevated root-zone salinity progressively decreases leaf size over time (Munns et al. 1988). This may be a direct effect of salt on rate of cell division, to a slower rate of expansion, or a decrease in the duration of expansion. If cell division was affected, even if cell growth potential was not affected, final leaf size would be limited due to reduced cell number. Cell division is undoubtedly affected by salt in suspension cell cultures, where individual cells are bathed in salt solution (e.g., Hasegawa et al. 1980). The impact of salt on cell division in whole plants is not well understood. For example, Munns et al. (1988) concluded that cell division in barley was not particularly sensitive to NaCl up to 175 mol m^{-3}. On the other hand, Bernstein et al. (1993) observed that salt (100 mol m^{-3} NaCl) shortened the growth zone in sorghum leaves, and at the same time reduced the maximal growth rate of cells in that region. They also noted that greatest sensitivity to salt was at the time of maximal elongation rate.

Root zone salinization also affects plant ontogeny. For example, Maas and Grieve (1990) and Grieve et al. (1994) reported that salt stress (140 mol m^{-3} NaCl) accelerated development of the wheat shoot apex on the main stem by as much as 18 d and decreased the time to initiation of reproductive structures. They, along with others (e.g., sweet clover [Romero and Maranon 1994a]), also reported a shorter time to flowering. Accelerated phenological development may not necessarily be a common response among all plant species, as demonstrated by Rawson (1986), who reported no change in phenology of barley in response to NaCl up to 150 mol m^{-3}. While it may hasten maturity, Grieve et al. (1993) found that salt (NaCl, 15.1 dS m^{-1}) decreased the rate of leaf primordium initiation without affecting the duration of this growth phase, thus leading to fewer leaves. By comparison, Grieve et al. (1993) found that salinity had no effect on the rate of spikelet primordium initiation, but the duration of this phase was shortened. Tiller development is delayed by salt by up to four days (Maas and Grieve 1990).

Root-zone salinity decreases the grain yield of spring wheat primarily by reducing the number of fertile tillers per plant (Maas and Grieve 1990; Hollington and Wyn Jones 1990; Silberbush and Lipps 1991). The magnitude of the reduction follows a declining function associated with increasing salinity (Maas et al. 1994; Hu 1996). Furthermore, subjecting spring wheat plants to saline rooting solutions early in their physiological development accentuates the decline (Maas and Poss 1989; Grieve et al. 1993; Francois et al. 1994).

Salinity affects the number of kernels and the kernel mass per spike proportionally less than salinity influences the number of tillers per plant (Grieve et al. 1993). Francois et al. (1994) also showed that the effect of salinity on kernel mass per spike was related to the time of salinization as well as the strength of the salt concentration. Salinity imposed early in the plant's development, but later withdrawn, had little impact on kernel mass. However, salinity imposed either late or throughout a plant's development significantly reduced the number of kernels per spike and changed the individual kernel mass. Maas and Grieve (1990) demonstrated similar effects, but noted that spring wheat grain mass per spike on the main stems remained nearly constant with root-zone salinity enrichments: the decrease in kernel numbers per spike was compensated by a tendency for an increase in kernel mass. Maas et al. (1996) further demonstrated that spring wheat, salinized after the plants had emerged, produce significantly fewer kernels per spike on the secondary tillers than within spikes borne on primary tillers and main stems.

The phenological responses to salt stress are clearly complex, but appear to produce fewer but higher quality seed in as short a time as possible. Nonetheless species and even varietal responses should not be used as generalized models for all plants. For example, Aloy (1992) found that in barley, grains per spike and spikes per unit area were quite insensitive to field-applied salinity, while 1000-seed weight was most strongly affected, accounting for most of the decrease in grain yield.

From Cell Death to Plant Death

New leaf growth is supported through the export of carbon from mature leaves. As the capacity of older leaves to furnish new leaf growth diminishes due to salt-induced leaf necrosis, the ability of new growth to handle the continuous export of salt from the root decreases. The salt-specific effects leading to premature senescence of older leaves represents the second phase of response of plants to salinization, the first phase is characterized by decreased leaf growth in response to more negative osmotic potential associated with concentrated solutes in the root zone (Munns 1994). In this second phase of salt response, the plant fairly quickly succumbs as a result of its ever-decreasing capacity to compartmentalize salt. In short, plant death occurs because the rate of leaf death overtakes rate of new leaf production. According to Munns (1994) differences in salt tolerance among genotypes are related to the difference in the time that it takes for salt to reach its maximum concentration in the leaf vacuoles. Thus, salt-sensitive plants are unable to compartmentalize salts in their leaves as effectively or to as high concentrations as can tolerant plants, and this may be exacerbated by faster rates of delivery of salt to the leaves.

MECHANISMS OF SALINITY TOLERANCE

Osmotic Adjustment

The collection of salt from the cytoplasm into the vacuole creates a strong osmotic gradient across the vacuolar membrane. This gradient is balanced by an increase in the synthesis of solute molecules in the cytoplasm, a process known as osmotic adjustment (Wyn Jones and Gorham 1983; McCue and Hanson 1990). Osmotic adjustment is regarded as an important adaption of plants to salinity because it helps to maintain turgor and cell volume. A variety of so-called compatible solutes have been identified, characterized as having roughly similar properties, a low polar charge, high solubility, and large hydration shell (Paleg et al. 1985). Because of these rather distinctive properties, apart from contributing to the maintenance of cell turgor, compatible solutes are believed to stabilize the active conformation of cytoplasmic enzymes, thereby protecting them against inactivation by inorganic ions (e.g., Pollard and Wyn Jones 1979; Smirnoff et al. 1990). Compatible solutes include compounds such as proline (Shen et al. 1994), glycine-betaine and other related quaternary ammonium compounds (Hanson and Burnet 1994), pinitol (Thomas and Bohnert 1993), mannitol (Everard et al. 1994) and sorbitol (Briens and Lahrer 1983). For example, in salt-stressed tobacco plants, proline synthesis increased up to 80 times (Rhodes and Handa 1989). Genetic evidence of the importance of glycine-betaine in enhancing salt tolerance has been demonstrated in barley and maize (Grumet and Hanson 1986; Saneoka et al. 1995). Similar evidence has been provided for mannitol, an important osmo-protectant in celery (Tarcynski et al. 1993).

However, the production of sufficient osmotica is metabolically expensive, potentially limiting the plant by consuming significant quantities of carbon that could otherwise be used for growth (Greenway and Munns 1980). The alternative to producing organic osmotica is to accumulate a high concentration of ions from the external medium. The energetic cost of osmotic adjustment by inorganic ions is much lower than that conferred by organic molecules synthesized in the cell (Wyn Jones 1981; Yeo 1993). This causes another problem because such high concentrations of toxic ions may interfere with normal biochemical activities within the cell (Polyjakoff-Mayber 1975). Osmotic adjustment might be an adaption for plants surviving under salt stress conditions but may also reduce growth due to ion toxicity, ion deficiency, and/or other physiological processes.

Salt Inclusion vs. Exclusion

It would appear that in glycophytes, the inability of the leaves to utilize the salt transported from the root at a pace commensurate with delivery leads to a slow leaf growth rate and eventually leaf death. There is a wealth of evidence linking exclusion of salt from the leaf with salt tolerance. This is especially true for many glycophytic species, includ-

ing crop plants such as wheat and barley (Gorham 1993), corn (Alberico and Cramer 1993), chickpea (Lauter and Munns 1987), beans (Awada et al. 1995), as well as for some halophytes (Richardson 1982; Harivandi et al. 1983; Gorham 1987, 1994). Salt exclusion from the shoot is, however, by no means the rule. The vast majority of halophytes use salt as an osmoticum to balance the concentration of the external medium (Ungar 1991). Moreover, there often appears to be no readily discernible relationship between salt exclusion and salt tolerance among many glycophytes. For example, while Na^+ exclusion was a general characteristic of a number of salt tolerant wheat lines, a salt sensitive line had much lower shoot Na^+ levels than the more tolerant lines (Schachtmann and Munns 1992). A similar observation was noted for maize, where a tolerant cultivar was reported to transport Na^+ to the shoot twice as fast as an intolerant cultivar (Cramer et al. 1994). Thus, insensitivity to salt is not necessarily due to an inability to exclude salt.

Na+/K+ Discrimination

Closely allied to salt exclusion and its relationship to salt tolerance is the regulation of ion selectivity, in particular the role of Na^+/K^+ discrimination, in salt tolerance (Gorham 1993). Na^+ can be substituted for K^+ for uptake, and it is believed that similar mechanisms of uptake may operate for both ions (Schroeder et al. 1994). High levels of K^+ in young expanding tissue is associated with salt tolerance in many plant species (Gorham 1993; Storey et al. 1993; Khatun and Flowers 1995). It is therefore possible that Na^+/K^+ discrimination is associated with salt tolerance.

Gorham (1993) claimed that all plants discriminate to some extent between Na^+ and K^+. Within the halophytic class of plants there appears to be a positive relationship between Na^+ inclusion and salt tolerance (e.g., Clipson and Flowers 1987). In such plants, K^+ accumulation accounts for barely 4% of total cation contribution to osmotic adjustment, and their Na^+/K^+ ratios may be as high as 30 in seawater-level salinity (Naidoo and Rughunanan 1991). On the other hand, Glenn et al. (1992) demonstrated that halophytes that appeared to discriminate against Na^+, in favour of K^+, were as tolerant of salt as those that appeared to favour Na^+ for osmotic adjustment. In the case of non-halophytes, it is clear that some species discriminate against Na^+ more than others by lowering $[Na^+]$ in the leaves, particularly in the cytoplasm, balanced by higher cytoplasmic K^+ concentrations, often increasing salt tolerance (Hajibagheri et al. 1989). The gene locus controlling Na^+/K^+ discrimination in *Triticum* has been identified (Gorham et al. 1987; Dvorak et al. 1994), and confers enhanced discrimination and, often, enhanced tolerance when introduced through recombination with related species (Gorham et al. 1991; Dvorak et al. 1992). Na^+/K^+ discrimination is, however, not a prerequisite for salt tolerance in glycophytes. For example, cultivated barley and some wild relatives of barley lack the enhanced Na^+/K^+ discrimination trait, even though it is recognized as being very tolerant to salt (Gorham 1993). Similarly, while some wild relatives of wheat tend to be better at discriminating against Na^+ than cultivated wheat, it is believed that this is not due to enhanced discrimination, but rather, to greater control of salt accumulation (Gorham 1994).

MEMBRANE TRANSPORT

Sustained plant growth under saline conditions requires strict and coordinated control of ion movement at the root-soil interface and at various control points along the plant leading up to and including the shoot meristem. Control is ultimately achieved via regulation of ion transport across the cell membrane. Understanding the principles of ion regulation at the membrane level may be useful for improving salt tolerance of crops.

Because of the hydrophobic nature of the plasma membrane, salt ions can only pass into the cell in the presence of thermodynamic gradients largely induced by the activity of proton pumps housed within the membrane. These pumps couple the free energy of hydrolysis of ATP or pyrophosphate to the transport of hydrogen ions (H^+) and generate an electrochemical gradient (Michelet and Boutry 1995) that moves salt ions across the plasma membrane. The plasma membrane-based proton pump directs the outward movement of H^+ ions, and thereby induces a net negative membrane potential inside the cell. Monovalent cations such as Na^+ move passively across the plasma membrane because of the internal negative membrane potential and are at equilibrium at internal concentrations of about 10 mol m^{-3} Na^+, and around 0.2 mol m^{-3} Ca^{2+} (Bush 1995). Typical cellular K^+ concentrations of 100–200 mol m^{-3} are achieved via active channels and porters (carriers). Channels and porters are distinct from pumps in that their function is not linked to a chemical reaction requiring enzyme activity. Channels are different from porters in that transport across the membrane occurs through a proteinaceous pore which opens and closes in response to chemical or environmental signals. Porters or carriers move solutes, either inorganic ions or organic molecules, across the membrane through a series of conformational changes in carrier proteins which first bind the molecule, transport it, and then release it at the other side (Hedrich and Schroeder 1989). Chloride concentrations of around 10 mol m^{-3} within the cell must be maintained by nonpassive carriers that overcome the negative internal charge.

An increase in external salt concentration widens the gradient driving the passive movement of Na^+ across the plasma membrane. The gradient is also increased by vacuolarization of cytoplasmic Na^+. Regulation of the rate of movement of sodium ions is accomplished through action of Na^+/H^+ antiporters housed in both the plasmalema and in the tonoplast (Blumwald et al. 1985; Dupont 1992). Antiporters operate in conjunction with the same H^+-ATPase pumps that function to establish the internal negative membrane potential. The movement of Na^+ outward from the membrane is coupled, through mediation of the antiporter, to outward movement of H^+. Evidence suggests that the presence of NaCl increases gene expression for proton pump activity (Niu et al. 1993) and that responsiveness of the membrane pump could be a measure of salt tolerance (Perez-Prat et al. 1994). The effectiveness of Na^+/H^+ antiporters in regulating cytoplasmic salt concentrations was demonstrated in tobacco cell culture where external NaCl concentrations of 428 mol

m^{-3} were balanced by 780 mol m^{-3} Na in the vacuole, and less than 100 mol m^{-3} Na in the cytoplasm (Binzel et al. 1988). Corroborative information about antiporters on salt-stressed carrot cell cultures has also been documented (Colombo and Cerana 1993).

The negative membrane potential of the plasma membrane deters entry of chloride ions into the cytoplasm. However, the passage of Na^+ ions across the membrane may shift the electrochemical potential toward passive entry of Cl^- ions through specific anion channels (Skerrett and Tyerman 1994). Compartmentalization of Cl^- ions may be achieved via anion channels driven by proton pump activity in the vacuolar membrane (Plant et al. 1994).

An initial response to high salt concentrations is the evacuation of salt ions from the cytoplasm through membrane-based efflux to the apoplast or vacuole via activation of H^+ pumps in the plasma membrane and vacuole. It is argued that this transitory state cannot be sustained for reasons that relate to energy inefficiencies (Schnapp et al. 1991). Tolerance is therefore probably contingent upon arrival at a new steady-state ion flux level that is associated with establishment of a new plasma membrane potential (Niu et al. 1995). The establishment of a different ion homeostasis would be mediated by changes in membrane proteins associated with ion transport, which themselves are responsive to a coordinated signal-transduction system. There is reasonable evidence that Ca^{2+} may serve as a secondary messenger, translating changes in external salt concentrations into a message that changes the mechanisms that regulate ion flux (Mendoza et al. 1994).

THE ROLE OF CALCIUM

Calcium ameliorates the adverse effects of salinity on plants (Lahaye and Epstein 1971; Ehret et al. 1990; Huang and Redmann 1995). Salinity impairs the uptake up Ca^{2+} by plants (Cramer et al. 1987), possibly by displacing it from the cell membrane (Lynch et al. 1987) or in some way affecting membrane function (Lauchli 1990). When this happens, the level of Na^+ in the leaf increases (Lauchli et al. 1994), and membrane K^+/Na^+ selectivity is impaired (Zhang and Lauchli 1995). Ca^{2+} amendment to salinized media up to a Na^+/Ca^{2+} ratio of around 5.7 reverses the effects of NaCl on plant growth (Maas and Grieve 1987). A direct effect of calcium on the extensibility of the cell wall has also been noted in a salinized halophyte (Rygol and Zimmermann 1990). When Ca^{2+} was applied to seven different salinized maize cultivars, those that took up the least Na^+ in the absence of Ca^{2+} showed the greatest increase in leaf growth rate in response to additional Ca^{2+} (Alberico and Cramer 1993). The authors concluded that Na^+ exclusion is not a reliable indicator of salt tolerance in maize. Magnesium and sodium sulfate salts in soil solution were found to reduce barley yield when cation activity ratios ($a_{Ca}/a_{\text{total cations}}$) were < 0.09 (Janzen and Chang 1987). Wild barley (*Hordeum jubatum)* was found to be more tolerant to saline ($MgSO_4$ and Na_2SO_4, 10–80 mol m^{-3}) solution culture and was less responsive to Ca^{2+}-amendment (Suhayda 1992; Huang et al. 1995). They suggested that the salinity-induced symptoms of cultivated barley may be the result of a Ca^{2+} deficiency, which were not evident in wild barley. By comparison, Huang and Redmann (1995) found that wild mustard (*Brassica kaber*) was less tolerant to sulfate salts of Mg and Na compared with canola (*Brassica napus* L. 'Excel'), and that this correlated with an increased responsiveness of wild mustard to Ca^{2+}-amendment. There has been at least one recent report in which salt had no effect on Ca^{2+} uptake by the plant, in this case sweet clover, and Ca^{2+} uptake actually increased during the plants reproductive phase (Romero and Maranon 1994b). Nonetheless, there seems to be positive evidence for the very important role of Ca^{2+} in maintaining ion homeostasis and growth under saline conditions.

THRESHOLD SALINITY TOLERANCE

Producers need to know how their crops will respond to saline soils. Threshold salinity tolerance is a concept developed by Maas and Hoffman (1977) to address this need. The concept infers a biphasic response to salt, whereby across some range of salt concentrations there is little decline in crop growth and yield is negligible, and above some threshold crop yield is inversely related to salt concentration. This pattern of influence is consistent with the framework of salt effects developed in this review. On the tolerance side of the inflection point, where yield is unaffected by salinity, the rate of delivery of salt to the shoot may be balanced by vacuolarization, which could conceivably be accomplished by retarding the influx of salt via exclusion at the root surface, or through growth which accommodates the influx of salt by producing more vacuoles.

Many environmental variables can shift the equilibrium towards a salt imbalance which would be expressed as a change in the threshold level characteristic of that crop. The positive influence of calcium on salinity tolerance through its protective role on membrane function is an example. If threshold levels of tolerance are a function of the environment, it is logical that tolerance will also be variable. Recent findings indicating extreme sensitivity of spring wheat to salinity under conditions of greenhouse sand culture (Hu 1996; Steppuhn and Wall 1996), suggest that the concept of static threshold tolerance levels characteristic of each crop species needs to be re-examined.

SUMMARY AND CONCLUSIONS

The constraints imposed by salinity on plants are initiated at the cellular level, where successful adaptation prevents salt ions from hindering normal biosynthetic processes. This response must be synchronized with the inward flux of solutes associated with salt uptake. Some plant species are clearly more flexible than others in these requirements for survival in salty environments. An understanding of how single cell responses to salt are coordinated with organismal and whole-plant responses to maintain an optimal balance between salt uptake and compartmentation is fundamental to our knowledge of how plants successfully adapt to salt stress. Our understanding of the processes underlying the visible manifestations of salt tolerance are still far from complete. The interpretation of the events that occur during

exposure of plants to saline media outlined in this review are subject to revision as our knowledge base on the topic expands.

Alberico, G. J. and Cramer, G. R. 1993. Is the salt tolerance of maize related to sodium exclusion? I. Preliminary screening of seven cultivars. J. Plant Nutr. 16: 2289–2303.

Aloy, M. 1992. Effect of different levels of salinity on yield and yield components of 6 varieties of barley. Proc. 2nd Congress, European Society of Agronomy, Warwick, UK.

Arif, H. and A. D. Tomos. 1993. Control of wheat leaf growth under saline conditions. Pages 45–52 *in* H. Lieth and A. Al Masoom, eds. Towards the rational use of high salinity tolerant plants. Vol. 2. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Awada, S., Campbell, W. F., Dudley, L. M. and Jurinak, J. J. 1995. Interactive effects of sodium chloride, sodium sulfate, calcium sulfate, and calcium chloride on snapbean growth, photosynthesis, and ion uptake. J. Plant Nutr. 18: 889–900.

Bernstein, L. and Hayward, H. E. 1958. Physiology of salt tolerance. Ann. Rev. Plant Physiol. 9: 25–46.

Bernstein, N., Silk, W. K. and Lauchli, A. 1993. Growth and development of sorghum leaves under conditions of NaCl stress. Planta 191: 433–439.

Binzel, M. I., Hess, F. D., Bressan, R. A. and Hasegawa, P. M. 1988. Intracellular compartmentation of ions in salt adapted tobacco cells. Plant Physiol. 86: 607–614.

Blumwald, E., Foster, M. G., Rea, P. A., Verma, D. P. S. and Poole, R. J. 1985. Presence of host-plasma membrane type H^+-ATPase in the membrane envelope enclosing the bacteroids in soybean root nodules. Plant Physiol. 78: 665–672.

Briens, M. and Lahrer, F. 1983. Sorbitol accumulation in Plantaginacieae: Further evidence for a function in stress tolerance. Z. Pflanzenphysiol. 110: 447–458.

Bush, D. S. 1995. Calcium regulation in plant cells and its role in signalling. Ann. Rev. Plant Physiol. Plant Mol. Biol. 46: 95–122.

Canny, M. J. 1995. Apoplastic water and solute movement: new rules for an old space. Annu. Rev. Plant Physiol. Plant Mol. Biol. 46: 215–236.

Clipson, N. J. W. and Flowers, T. J. 1987. Salt tolerance in the halophyte *Suaeda maritima* L. Dum. The effect of salinity on the concentration of sodium in the xylem. New Phytol. 105: 359–366.

Clipson, N. J. W., Tomos, A. D., Flowers, T. J. and Wyn Jones, R. G. 1985. Salt tolerance in the halophyte *Suaeda maritima* L. Dun. Planta 165: 392–396.

Colombo, R. and Cerana, R. 1993. Enhanced activity of tonoplast pyrophosphatase in NaCl-grown cells of *Daucus carota*. J. Plant Physiol. 142: 226–229.

Cosgrove, D. J. 1986. Biophysical control of plant cell growth. Ann. Rev. Plant Physiol. 37: 377–405.

Cramer, G. R. and Bowman, D. C. 1991. Kinetics of maize leaf elongation. I. Increased yield threshold limits short-term, steady-state elongation rates after exposure to salinity. J. Exp. Bot. 42: 1417–1426.

Cramer, G. R., Alberico, G. J. and Schmidt, C. 1994. Salt tolerance is not associated with the sodium accumulation of two maize hybrids. Aust. J. Plant Physiol. 21: 675–692.

Cramer, G. R., Lynch, J., Lauchli, A. and Epstein, E. 1987. Influx of Na^+, K^+, and Ca^{2+} into roots of salt stressed cotton seedlings. Effects of supplemental Ca^{2+}. Plant Physiol. 79: 171–176.

Dupont, F. M. 1992. Salt-induced changes in ion transport: Regulation of primary pumps and secondary transporters. Pages 91–100 *in* D. T. Cooke and D. T. Clarkson, eds. Transport and receptor proteins of plant membranes. Plenum Press, New York, NY.

Dvorak, J., Epstein, E., Galavez, A., Gulick, P. J. and Omielan, J. A. 1992. Genetics of the physiological and molecular mechanisms associated with the salt tolerance in wheat and *Lophopyrum elongatum*. Pages 125–136 *in* Proc. International Conference on Agricultural Management in Salt-affected areas. Agadir, Morocco, 26 April–3 May 1991.

Dvorak, J., Noaman, M. M., Goyal, S. and Gorham, J. 1994. Enhancement of the salt tolerance of *Triticum turgidum* L. by the Knal locus transferred from the *Triticum aestivum* L. Chromosome 4D by homoeologous recombination. Theor. Appl. Genet. 88: 872–877.

Ehret, D. L., Remann, R. E., Harvey, B. L. and Cipywnyk, A. 1990. Salinity-induced calcium deficiencies in wheat and barley. Plant Soil 128: 143–151.

Everard, J. D., Gucci, R., Kann, S. C., Flore, J. A. and Loescher, W. H. 1994. Gas exchange and carbon partitioning in the leaves of celery *Apium graveolens* L. at various levels of root zone salinity. Plant Physiol. 106: 282–292.

Flowers, T. J., Hajibagheri, M. A. and Clipson, J. W. 1986. Title? Q. Rev. Biol. 61: 313.

Francois, L. E., Grieve, C. M., Maas, E. V. and Lesch, S. M. 1994. Time of salt stress affects growth and yield components of irrigated wheat. Agron. J. 86: 100–107.

Glenn, E. P., Watson, M. C., O'Leary, J. W. and Axelson, R. D. 1992. Comparison of salt tolerance and osmotic adjustment of low-sodium and high-sodium subspecies of the C4 halophyte, Atriplex canescens. Plant, Cell Environ. 15: 711–718.

Gorham, J. 1987. Photosynthesis, transpiration and salt fluxes through leaves of *Leptochloa fusca* L. Kunth. Plant, Cell Environ. 10: 19–26.

Gorham, J. 1993. Genetics and physiology of enhanced K/Na discrimination. Pages 151–159 *in* P. Randall, ed. Genetic aspects of plant mineral nutrition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gorham, J. 1994. Salt tolerance in the Triticae: K/Na discrimination in some perennial wheatgrasses and their amphiploids with wheat. J. Exp. Bot. 45: 441–447.

Gorham, J., Bristol, A., Young, E. M. and Wyn Jones, R. G. 1991. Presence of the enhanced K/Na discrimination trait in diploid Triticum species. Theor. Appl. Genet. 82: 729–736.

Gorham, J., Hardy, C., Wyn Jones, R. G., Joppa, L. R. and Law, C. N. 1987. Chromosomal location of a K/Na discrimination character in the D genome of wheat. Theor. Appl. Genet. 74: 584–588.

Greenway, H. and R. Munns. 1980. Mechanism of salt tolerance in nonhalophytes. Ann. Rev. Plant Physiol. 31: 149–190.

Greenway, H. and Osmond, C. B. 1972. Salt responses of enzymes from species differing in salt tolerance. Plant Physiol. 49: 256–259.

Grieve, C. M., Francois, L. E. and Maas, E. V. 1994. Salinity affects the timing of phasic development in spring wheat. Crop Sci. 34: 1544–1549.

Grieve, C. M., Lesch, S. M., Maas, E. V. and Francois, L. E. 1993. Leaf and spikelet primordia initiation in salt-stressed wheat. Crop Sci. 33: 1286–1292.

Grumet, R. and Hanson, A. D. 1986. Genetic evidence of an osmoregulatory function of glycine-betaine accumulation in barley. Aust. J. Plant Physiol. 13: 356–364.

Hajibagheri, M. A., Yeo, A. R., Flowers, T. J. and Collins, J. C. 1989. Salinity resistance in *Zea mays*: fluxes of potassium, sodium and chloride, cytoplasmic concentrations and microsomal membrane lipids. Plant, Cell and Environ. 12: 753–757.

Hanson, A. D. and Burnet, M. 1994. Evolution and metabolic engineering of osmoprotectant accumulation in higher plants.

Pages 291–302 *in* J. H. Cherry, ed. Biochemical and cellular mechanisms of stress tolerance in plants. NATO Series, Vol H86. Springer-Verlag, Berlin, Germany.
Harivandi, M. A., Butler, J. D. and Soltanpour, P. N. 1983. Effects of soluble salts on ion accumulation in *Puccinellia* spp. J. Plant Nutr. 6: 255–264.
Hasegawa, P. M., Bressan, R. A. and Handa, A. K. 1980. Growth characteristics of NaCl-selected and nonselected cells of *Nicotiana tabacum* L. Plant Cell Physiol. 21: 1347–1355.
Hedrich, R. and Shroeder, J. I. 1989. The physiology of ion channels and electrogenic pumps in higher plants. Ann. Rev. Plant Physiol. 40: 539–556.
Hollington, P. A. and Wyn Jones, R. G. 1990. The effect of variable salinity on the yield and yield components of wheat cultivars and an amphidiploid between wheat and *Thinopyrum bessarabicum*. Proc. 1st Congress, European Society of Agronomy, Paris, France.
Hu, Y. 1996. Growth response of wheat plant to salinity in hydroponics and soil. PhD. Dissertation, No. ETH 11619, Swiss Federal Institute of Technology, Zurich, Switzerland, 129 p.
Huang, J. and Redmann, R. E. 1995. Responses of growth, morphology, and anatomy to salinity and calcium supply in cultivated and wild barley. Can. J. Bot. 73: 1859–1866.
Janzen, H. H. and Chang, C. 1987. Cation nutrition of barley as influenced by soil solution composition in a saline soil. Can. J. Soil Sci. 67: 619–629.
Khatun, S. and Flowers, T. J. 1995. Effect of salinity on seed set in rice. Plant, Cell Environ. 18: 61–87.
Lahaye, P. A. and Epstein, E. 1971. Calcium and salt toleration by bean plants. Physiol Plant. 25: 213–218.
Lauchli, A. 1990. Calcium, salinity and the plasma membrane. Curr. Topics Plant Physiol. 4: 26–35.
Lauchli, A., Colmer, T. D., Fan, T. W. -M. and Higashi, M. 1994. Solute regulation by calcium in salt-stressed plants. Pages 443–461 *in* J. H. Cherry, ed. Biochemical and cellular mechanisms of stress tolerance in plants. Springer-Verlag, Berlin, Germany.
Lauter, D. L. and Munns, D. N. 1986. Salt resistance of chickpea genotypes in solutions salinized with NaCl or Na_2SO_4. Plant Soil 95: 271–279.
Lloyd, J., Syvertsen, J. P. and Kriedemann, P. E. 1987. Salinity effects on leaf water relations and gas exchange of "Valencia" orange, *Citrus sinensis* L. Osbeck, on root stocks with different salt exclusion characteristics. Aust. J. Plant Physiol. 14: 605–617.
Lockhart, J. A. 1965. An analysis of irreversible plant cell elongation. J. Theor. Biol. 8: 264–275.
Lynch, J., Cramer, G. O. and Lauchli, A. 1987. Salinity reduces membrane-associated calcium in corn root protoplasts. Plant Physiol. 83: 390–394.
Maas, E. V. and Grieve, C. M. 1987. Sodium-induced calcium deficiency in salt-stressed corn. Plant, Cell Environ. 10: 559–564.
Maas, E. V. and Grieve, C. M. 1990. Spike and leaf development in salt-stressed wheat. Crop Sci. 30: 1309–1313.
Maas, E. V. and Hoffman, G. J. 1977. Crop salt tolerance-current assessment. J. Irrig. Drain. Div. Am. Soc. Civil Eng. 103IR2: 115–134.
Maas, E. V. and Poss, J. A. 1989. Salt sensitivity of wheat at various growth stages. Irrig. Sci. 10: 29–40.
Maas, E. V. Lesch, S. M., Francois, L. E. and Grieve, C. M. 1994. Tiller development in salt-stressed wheat. Crop Sci. 34: 1594–1603.
Maas, E. V., Lesch, S. M., Francois, L. E. and Grieve, C. M. 1996. Contribution of individual culms to yield of salt-stressed wheat. Crop Sci. 36: 142–149.
McCree, K. J. 1986. Whole-plant carbon balance during osmotic adjustment to drought and salinity stress. Pages 33–34 *in* N. C. Turner and J. B. Passioura, eds. Plant growth, drought and salinity. CSIRO, Melbourne, Australia.
McCue, K. F. and Hanson, A. D. 1990. Drought and salt tolerance: towards an understanding and application. Trends Biotechnol. 8: 358–362.
Mendoza, I., Rubio, F., Rodriguez-Navarro, A. and Pardo, J. M. 1994. The protein phosphatase calcineurin is essential for NaCl tolerance of Saccharomyces cerevisiae. J. Biol Chem. 269: 8792–8796.
Michelet, B. and Boutry, M. 1995. The plasma membrane H^+-ATPase. A highly regulated enzyme with multiple physiological functions. Plant Physiol. 108: 1–6.
Munns, R. 1994. Physiological processes limiting growth in saline soils: some dogmas and hypotheses. Plant, Cell Environ. 16: 15–24.
Munns, R. and Termaat, A. 1986. Whole plant responses to salinity. Aust. J. Plant Physiol. 13: 143–160.
Munns, R., Gardner, A., Tonnet, M. L. and Rawson, H. M. 1988. Growth and development in NaCl-treated plants. II. Do Na^+ or Cl^- concentrations in dividing or expanding tissues determine growth in barley? Aust. J. Plant Physiol. 15: 529–540.
Myers, B. A., Neales, T. F. and Jones, M. B. 1990. The influence of salinity on growth, water relations and photosynthesis in *Ciplachne fusca* L. P. Beauv. ex Roemer and Schultes. Aust. J. Pl. Physiol. 17: 675–691.
Naidoo, G. and Rughunanan, R. 1991. Salt tolerance in the succulent, coastal halophyte, *Sarcocornia natalensis*. J. Exp. Bot. 41: 497–502.
Neumann, P. M. 1993. Rapid and reversible modifications of extension capacity of cell walls in elongating maize leaf tissues responding to root addition and removal of NaCl. Plant, Cell Environ. 16: 1107–1114.
Neumann, P. M., Azaizeh, H. and Leon, D. 1994. Hardening of root cell walls: a growth inhibitory response to salinity stress. Plant, Cell Environ. 17: 303–309.
Newmann, I. A. and Azaizeh, H. 1994. Hardening of root cell walls, a growth inhibiting response to salinity stress. Plant, Cell Environ. 17: 303–309.
Niu, X., Narasimhan, Salzman, R. A., Bressan, R. A. and Hasegawa, P. M. 1993. NaCl regulation of plasma membrane H^+-ATPase gene expression in a glycophyte and a halophyte. Plant Physiol. 103: 713–718.
Niu, X., Bressan, R. A., Hasagawa, P. M. and Pardo, J. M. 1995. Ion homeostasis in NaCl stress environments. Plant Physiol. 109: 735–742.
Paleg, L. G., Stewart, G. R. and Starr, R. 1985. The effect of compatible solutes on proteins. Plant Soil 89: 46–57.
Perez-Prat, E., Narasimhan, M. I., Niu, X., Botella, M. A., Bressan, R. A., Valpuesta, V., Hasegawa, P. M. and Binzel, M. L. 1994. Growth cycle stage-dependent NaCl induction of plasma membrane H^+-ATPase mRNA accumulation in de-adapted tobacco cells. Plant Cell Environ. 17: 327–333.
Plant, P., Gelli, A. and Blumwald, E. 1994. Vacuolar chloride regulation of an anion-selective tonoplast channel. J. Membr. Biol. 140: 1–12.
Poljakoff-Mayber, A. 1975. Morphological and anatomical changes in plants as a response to salinity stress. Pages 97–117 *in* A. Poljakoff-Mayber and J. Gale, eds. Plants in saline environments. Ecological Series 15. Springer-Verlag, Berlin, Germany.
Pollard, A. and Wyn Jones, R. G. 1979. Enzyme activities in concentrated solutions of glycine betaine and other solutes. Plant 14: 292–298.
Pritchard, J., Wyn Jones, R. G. and Tomos, A. D. 1991. Turgor, growth and rheological gradients of wheat roots following osmotic stress. J. Exp. Bot. 42: 1043–1049.

Randall, H. C. and Sinclair, T. C. 1989. Leaf wall yield threshold of field-grown soybean measured by vapour pressure psychrometry. Plant, Cell Environ. 12: 441–447.
Rawson, H. M. 1986. Gas exchange and growth in wheat and barley grown in salt. Aust. J. Plant Physiol. 13: 475–489.
Rhodes, D. and Handa, S. 1989. Amino acid metabolism in relation to osmotic adjustment in plant cells. Pages 41–62 *in* J. H. Cherry, ed. Environmental stress in plants. Biochemical and physiological mechanisms. NATO ASI Series, Vol G19, Springer-Verlag, Berlin, Germany.
Richardson, S. G. 1982. High and low sodium biotypes of fourwing saltbush: their responses to sodium and potassium in tectorated oil shale. J. Range Manage 35: 795–803.
Romero, J. M. and Maranon, T. 1994a. Long-term responses of *Melilotus segitalis* to salinity. I. Growth and partitioning. Plant, Cell Environ. 17: 1243–1248.
Romero, J. M. and Maranon, T. 1994b. Long-term responses of *Melilotus segitalis* to salinity. II. Nutrient absorption and utilization. Plant, Cell Environ. 17: 1249–1255.
Rygol, J. and Zimmermann, U. 1990. Radial and axial turgor pressure measurements in individual root cells of *Mesembryanthemum crystallinum* grown under various saline conditions. Plant, Cell Environ. 13: 15–26.
Saneoka, H., Nagasaka, C., Hahn, D. T., Yang, W., Premachandra, G. S., Joly, R. J., Schactman, D. P. and Munns, R. 1992. Sodium accumulation in leaves of *Triticum* species that differ in salt tolerance. Aust. J. Plant Physiol. 19: 331–340.
Schnapp, S. R., Curtin, W. R., Bressan, R. A. and Hasegawa, P. M. 1991. Growth yields and maintenance coefficients of unadapted and NaCl-adapted tobacco cells grown in semicontinuous culture. Plant Physiol. 96: 1289–1293.
Schroeder, J. I., Ward, J. M. and Gassmann, W. 1994. Perspectives on the physiology and structure of inward-rectifying K^+ channels in higher plants: biophysical implications for K^+ uptake. Ann. Rev. Biophys. Biomol. Struct. 23: 441–471.
Shen, Z., Shen, Q., Liang, Y. and Liu, Y. 1994. Effect of nitrogen on the growth and photosynthetic activity of salt-stressed barley. J. Plant Nutr. 17: 787–799.
Silberbush, M. and Lipps, S. H. 1991. Potassium, ammonium/nitrate ratio, and sodium chloride effects on wheat growth. II. Tillers and grain yield. J. Plant Nutr. 14: 765–773.
Skerrett, M. and Tyerman, S. D. 1994. A channel that allows inwardly directed fluxes of anions in protoplast derived from wheat roots. Planta 192: 295–305.
Smirnoff, C., Thonke, B. and Popp, M. 1990. The compatibility of D-pinitol and 1D-1-O-methyl-mucoinositol with malate dehydrogenase activity. Bot. Acta 103: 270–273.
Steppuhn, H. and K. Wall. 1996. Relative salt tolerances of four spring-sown wheats. Pages 1–7 *in* Proc. Dryland Salinity Workshop "Causes to Cures", Prairie Salinity Network, Alberta Agriculture, Lethbridge, AB.
Storey, R., Gorham, J., Pitman, M. C., Hanson, M. G. and Gage, D. 1993. Response of *Melanthera biflora* to salinity and water stress. J. Exp. Bot. 44: 1551–1561.
Suhayda, C. G., Redmann, R. E., Harvey, B. L. and Cipywnyk, A. L. 1992. Comparative response of cultivated and wild barley species to salinity stress and calcium supply. Crop Sci. 32: 154–163.
Tarcynski, M. C., Jensen, R. G. and Bohnert, H. J. 1993. Stress protection of transgenic tobacco by production of the osmolyte mannitol. Science 259: 508–510.
Thomas, J. C. and Bohnert, H. J. 1993. Salt stress perception and plant growth regulation in the halophyte *Mesembryanthemum crystalinum*. Plant Physiol. 103: 1299–1304.
Ungar, I. A. 1991 Ecophysiology of vascular halophytes. CRC Press, Boca Raton, FL. 209 pp.
Winter, H., Robinson, D. G. and Heldt, H. W. 1993. Subcellular volumes and metabolite concentrations in barley leaves. Planta 191: 180–190.
Wyn Jones, R. G. 1981. Salt tolerance. Pages 271–292 *in* C. B. Johnson, ed. Physiological processes limiting plant productivity. Butterworths, London, UK.
Wyn Jones, R. G. and Gorham, J. 1983. Osmoregulation. Pages 35–38 *in* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds. Physiological plant ecology. III. Encyclopaedia of Plant Physiology. Vol. 12C. Springer-Verlag, Berlin, Germany.
Yeo, A. R. 1983. Salinity resistance: physiologies and prices. Physiol. Plant 58: 214–222.
Zhang, H. and Lauchli, A. 1994. Spatial distribution of solutes, K, Na, Ca and their deposition rates in the growth zone of primary cotton roots. Effects of NaCl and $CaCl_2$. Planta 194: 34–41.