

Salt Tolerance and Crop Potential of Halophytes

Edward P. Glenn and J. Jed Brown

Environmental Research Laboratory, 2601 East Airport Drive, Tucson, Arizona 85706

Eduardo Blumwald

University of Toronto, Toronto, Ontario, Canada, M5S 3B2

ABSTRACT: Although they represent only 2% of terrestrial plant species, halophytes are present in about half the higher plant families and represent a wide diversity of plant forms. Despite their polyphyletic origins, halophytes appear to have evolved the same basic method of osmotic adjustment: accumulation of inorganic salts, mainly NaCl, in the vacuole and accumulation of organic solutes in the cytoplasm. Differences between halophyte and glycophyte ion transport systems are becoming apparent. The pathways by which Na⁺ and Cl⁻ enters halophyte cells are not well understood but may involve ion channels and pinocytosis, in addition to Na⁺ and Cl⁻ transporters. Na⁺ uptake into vacuoles requires Na⁺/H⁺ antiporters in the tonoplast and H⁺ ATPases and perhaps PP_i ases to provide the proton motive force. Tonoplast antiporters are constitutive in halophytes, whereas they must be activated by NaCl in salt-tolerant glycophytes, and they may be absent from salt-sensitive glycophytes. Halophyte vacuoles may have a modified lipid composition to prevent leakage of Na⁺ back to the cytoplasm.

Because of their diversity, halophytes have been regarded as a rich source of potential new crops. Halophytes have been tested as vegetable, forage, and oilseed crops in agronomic field trials. The most productive species yield 10 to 20 ton/ha of biomass on seawater irrigation, equivalent to conventional crops. The oilseed halophyte, *Salsicornia bigelovii*, yields 2 t/ha of seed containing 28% oil and 31% protein, similar to soybean yield and seed quality. Halophytes grown on seawater require a leaching fraction to control soil salts, but at lower salinities they outperform conventional crops in yield and water use efficiency. Halophyte forage and seed products can replace conventional ingredients in animal feeding systems, with some restrictions on their use due to high salt content and antinutritional compounds present in some species. Halophytes have applications in recycling saline agricultural wastewater and reclaiming salt-affected soil in arid-zone irrigation districts.

KEY WORDS: salt stress, saline water irrigation, seawater crops, osmotic adjustment, sodium uptake.

I. INTRODUCTION

In 1980 it was predicted that genetic manipulation would lead to breakthroughs in crop production on saline water such that ordinary crops like barley and tomato could be grown on seawater (Epstein et al., 1980). However, recent assessments have been gloomy. One review points out that from 1980 to 1995 over 300 papers a year were published on mechanisms of salt tolerance in higher plants, yet fewer than a dozen salt-tolerant cultivars were

released, offering only slight improvement over the parent lines (Flowers and Yeo, 1995). In fact, it has been questioned whether any cultivars bred for salt tolerance have been commercially successful. Farmers are still better off planting yield-selected rather than salt-selected lines in salty soils (Richards, 1992). Two leading biochemists who take a molecular approach to salt-tolerance research called for a moratorium on further plant breeding until the molecular genetics are better understood (Bohnert and Jensen, 1996); a leading breeder who takes a

physiological approach responded that molecular biologists project "...the optimism of blue skies researchers advertising their wares" (reply by Flowers in Bohnert and Jensen, 1996).

Almost all our modern crops are derived from glycophytes, plants apparently lacking the genetic basis for salt tolerance, and they have received the most research attention. All sides now call for a better understanding of how naturally adapted plants (halophytes) handle salts. Study of halophytes can be instructive from three perspectives. First, the mechanisms by which halophytes survive and maintain productivity on saline water can be used to define a minimal set of adaptations required in tolerant germplasm. This knowledge can help to focus the efforts of plant breeders and molecular biologists working with conventional crop plants (Bohnert et al., 1995; Glenn et al., 1997b; Niu et al., 1995; Rausch et al., 1996; Serrano, 1996; Serrano and Gaxiola, 1994; Zhu et al., 1997). Second, halophytes grown in an agronomic setting can be used to evaluate the overall feasibility of high-salinity agriculture, which depends on more than finding a source of tolerant germplasm (Glenn et al., 1997a; Miyamoto, 1996; Miyamoto et al., 1996; Rhoades, 1993; van Schilfgaarde, 1993). Third, halophytes may become a direct source of new crops (Aronson, 1989; Boyko and Boyko, 1959; Boyko, 1966; Somers, 1975; Choukr-Allah et al., 1996; Glenn et al., 1991, 1997a; Llerena, 1994; O'Leary, 1994; Squires and Ayoub, 1994). After briefly considering the diversity of halophytes, we review the current understanding of halophyte salt-tolerance mechanisms and their relevance to efforts to improve crop plants and the status of halophyte agronomy.

II. DIVERSITY OF HALOPHYTES

Halophytes are considered to be rare plant forms that arose separately in unrelated plant families during the diversification of angiosperms (O'Leary and Glenn, 1994); in this they resemble epiphytes, saprophytes, xero-

phytes, aquatics, and marsh plants (Kremer and VanAndel, 1995). No comprehensive list of halophyte species exists, due partly to the problem of defining the lower salt-tolerance limit at which a plant should be considered a halophyte. Aronson (1989) compiled a partial list of halophytes containing 1560 species in 550 genera and 117 families. His list was drawn from literature reports and interviews with researchers as part of a program to assemble a world halophyte collection to screen for new crops (Aronson et al., 1988). He used a broad definition of halophyte that included any plant that was reportedly more tolerant than conventional crops, for which the upper salt content of irrigation water was taken to be 5 g/l total dissolved solids (TDS) (85 mM as NaCl) (Ayers and Wescott, 1989). However, his list only included plants that had potential as food, forage, fuelwood, or soil stabilization crops.

Based on a comparison of Aronson's entries with the known number of species in selected halophytic genera, Le Houerou (1993) estimated that Aronson's list probably included 20 to 30% of the terrestrial halophytic flora, which would then reach 5000 to 6000 species, or 2% of world angiosperm species. Of the species in the list, 57% came from just 13 families. The largest number of halophyte species are in the Chenopodiaceae; over half of its 550 species are halophytic. The three superfamilies, Poaceae (grasses), Fabaceae (legumes), and Asteraceae (composites), also have large numbers of halophytes, although they represent fewer than 5% of the species in these families. These families proliferated through radiative evolution into many diverse niches, including saline habitats, during the early evolution of angiosperms. Flowers et al. (1977) plotted the occurrence of halophytes in the major orders of flowering plants in a dendrogram showing probable relationships between orders. Halophytes occurred throughout the dendrogram in both primitive (e.g., Laurales, Nymphales) and advanced (Asterales, Orchidales) orders.

In keeping with their multiple origins, halophytes differ widely in their degree of salt tol-

erance (Flowers et al., 1977; Ungar, 1991). Aronson's (1989) list can be viewed as a pyramid, with the base consisting of several thousand species exhibiting modest tolerance, narrowing toward the top to perhaps a few dozen species capable of high production on seawater. At the low end of the salt-tolerance scale, some crop plants such as sugar beet (*Beta vulgaris*, Chenopodiaceae), date palm (*Phoenix dactylifera*, Arecaceae) and barley (*Hordeum vulgare*, Poaceae) can be cultivated on irrigation water approaching 5 g/l TDS (Ayers and Wescott, 1989) and are sometimes considered halophytes. At the upper end, species such as *Salicornia bigelovii* (Chenopodiaceae) can yield as much biomass and seed as conventional crops even when the soil solution exceeds 70 g/l TDS (1.3 M as NaCl, twice seawater salinity) (Glenn et al., 1991, 1997). The continuous nature of the salt-tolerance gradient extends downward through the glycophytes as well, eventually reaching the most sensitive crops such as rice and bean, which are harmed by 20 to 50 mM NaCl (Greenway and Munns, 1980).

Halophytes also differ widely in their apparent adaptations to handle salts (Ungar, 1991). Classification schemes have been constructed that attempt to match morphological and physiological characters to specific halophyte habitats or growth strategies. Le Houerou (1993) reviewed three schemes that divided halophytes into 4 types based on the degree of salt tolerance, 5 types based on ecological associations, and 12 types based on edaphic factors. However, these classification systems have little predictive value. For example, a recent study attempted to correlate leaf anatomy with zonation of 13 halophytes along a transect in a salt marsh in Jordan (Weiglin and Winter, 1991). The purpose was to determine if species with xeromorphic leaves were distributed differently than those with mesomorphic leaves; the species along the transect differed as well in photosynthetic pathway (C_3 or C_4), degree of succulence, and numerous other traits, and were variously classified as euhalophytes (true halophytes), psuedohalophytes (salt avoiders),

or crinohalophytes (salt excretors). All combinations of plant types coexisted at 9 of the 11 stations along the transect, and the authors concluded there was no correlation between position in the marsh and leaf morphology or any of the other traits measured in this study.

Earlier studies reported that salt marsh halophytes can be divided into physiotypes based on their shoot water content and tendency to accumulate ions, but the physiotype concept could not be used to predict salt tolerance or zonation in the marsh (Albert and Popp, 1977; Storey et al., 1977; Gorham et al., 1980). Salt excretion is a well-known example of contrasting traits; black mangroves (*Avicennia* spp.) have well-developed salt glands that appear to function in salt tolerance by allowing the plant to excrete excess salts onto the leaf surface; yet, the equally salt-tolerant red mangroves (*Rhizophora* spp.) excrete no salt at all (Popp et al., 1993).

The taxonomic diversity of halophytes raises the possibility that salt tolerance might be introduced into crop plants through wide crosses (Epstein et al., 1980). Crops with salt-tolerant, wild relatives include wheat (related to *Aegilops*, *Thinopyrum*, and other wild members of the Triticeae) (Gorham and Wyn-Jones, 1993), barley (related to sea oats, *Hordeum maritimum*) (Aronson, 1989), tomato (related to wild, salt-tolerant tomatoes, including *Lycopersicon cheesmanii* and *L. pimpinellifolium*) (Asins et al., 1993), and fodderbeet (*Beta vulgaris* ssp. *vulgaris*, related to seabed, *B. vulgaris* ssp. *maritima*) (Rozema et al., 1993). The feasibility of transferring salt tolerance between species has been demonstrated for wheat, a glycophyte. A gene (+Knal) for enhanced K^+/Na^+ discrimination was transferred from bread wheat (*Triticum aestivum*) to durum wheat (*T. turginsum*) using conventional crossing, with the hybrid plants exhibiting slightly improved salt tolerance (Dvorak et al., 1994). Similarly, salt tolerance genes from *Triticum tauschii* were expressed in hexaploid wheat (Schachtman et al., 1992). However, the hope for improving salt tolerance in large steps

through glycophyte-halophyte crosses has so far not been fulfilled, attributed to the multigenic nature of halophyte salt tolerance (Flowers and Yeo, 1995).

Given their diverse origins, any trait that turns out to be universally present in halophytes should be suspected to represent convergent evolution of an essential trait for salt tolerance. Such a trait should be singled out for scrutiny as a candidate for eventual transfer from halophytes to glycophytes (Bohnert et al., 1995; Niu et al., 1995; Serrano, 1996; Zhu et al., 1997). We attempt to identify such traits in the next section. Also by their diversity, halophytes offer a rich source of germplasm to search for new crops as well as useful genes. At least a few species might be expected to have desirable crop characteristics that can be enhanced through conventional breeding to make them useful for agriculture. Halophytes have the advantage of being preadapted to salt tolerance, which has proven so difficult to introduce into glycophytes (O'Leary, 1994).

III. SALT TOLERANCE MECHANISMS OF HALOPHYTES

A. Physiology of Halophyte Salt Tolerance

In contrast to the situation with glycophytes, for which salt tolerance mechanisms are still vigorously debated (Wyn Jones and Gorham, 1986; Munns, 1993; Neumann, 1997), a clear picture of the physiology of halophyte salt tolerance has emerged, and several key enzyme systems and genetic control mechanisms have been identified. The basic nature of halophyte salt tolerance was described in a 1977 review article (Flowers et al., 1977) that is still widely cited, although it has been updated (Flowers and Yeo, 1986, 1988). Halophytes use the controlled uptake of Na^+ (balanced by Cl^- and other anions) into cell vacuoles to drive water into the plant against a low external water potential.

Dicotyledonous halophytes generally accumulate more NaCl in shoot tissues than monocotyledonous halophytes (especially grasses), which led early researchers to characterize the former as “includers” and the latter as “excluders” (Greenway, 1968; Ahmad et al., 1981a,b). The enhancement of exclusion mechanisms still appears to be the principal strategy of researchers trying to improve the salt tolerance of grains (Ashraf, 1994; Dvorak et al., 1994; Rubio et al., 1995; Schachtman et al., 1992; Yeo, 1994), even though Greenway corrected his earlier characterization of grasses as strict excluders in 1980 (Greenway and Munns, 1980). Studies of *Spartina alterniflora* (Bradley and Morris, 1991), *Leptochloa fusca* (Jeschke et al., 1995), *Sporobolus virginicus* (Blits and Gallagher, 1991; Marcum and Murdoch, 1992), barley (Fricke et al., 1996), *Plantago* spp. (Erdei and Kuiper, 1979) and *Triglochin* spp. (Naidoo, 1994) show that grasses and other monocotyledonous halophytes use Na^+ uptake into leaves for osmotic adjustment, as do dicot halophytes. Because of their lower cell vacuolar volume and leaf water content, grasses do not need as much Na^+ uptake per unit of growth as typical dicotyledonous halophytes, so they maintain lower Na:K ratios on exposure to salt, but with a few exceptions (e.g., Matsushita and Matoh, 1992) they are not strict excluders (Glenn, 1987).

B. Performance of Halophytes on a Salinity Gradient

The central role of Na^+ uptake in determining the salt tolerance of halophytes is illustrated in Figures 1 and 2, which summarize results from 20 dicotyledonous (Glenn and O'Leary, 1984) and 27 monocotyledonous halophytes (Glenn, 1987) screened under similar conditions along a salinity gradient. The plants were assembled from a world collection of species reportedly exhibiting unusual salt tolerance, and spanned the range from essentially glycophytic species such as wheat and sunflower to

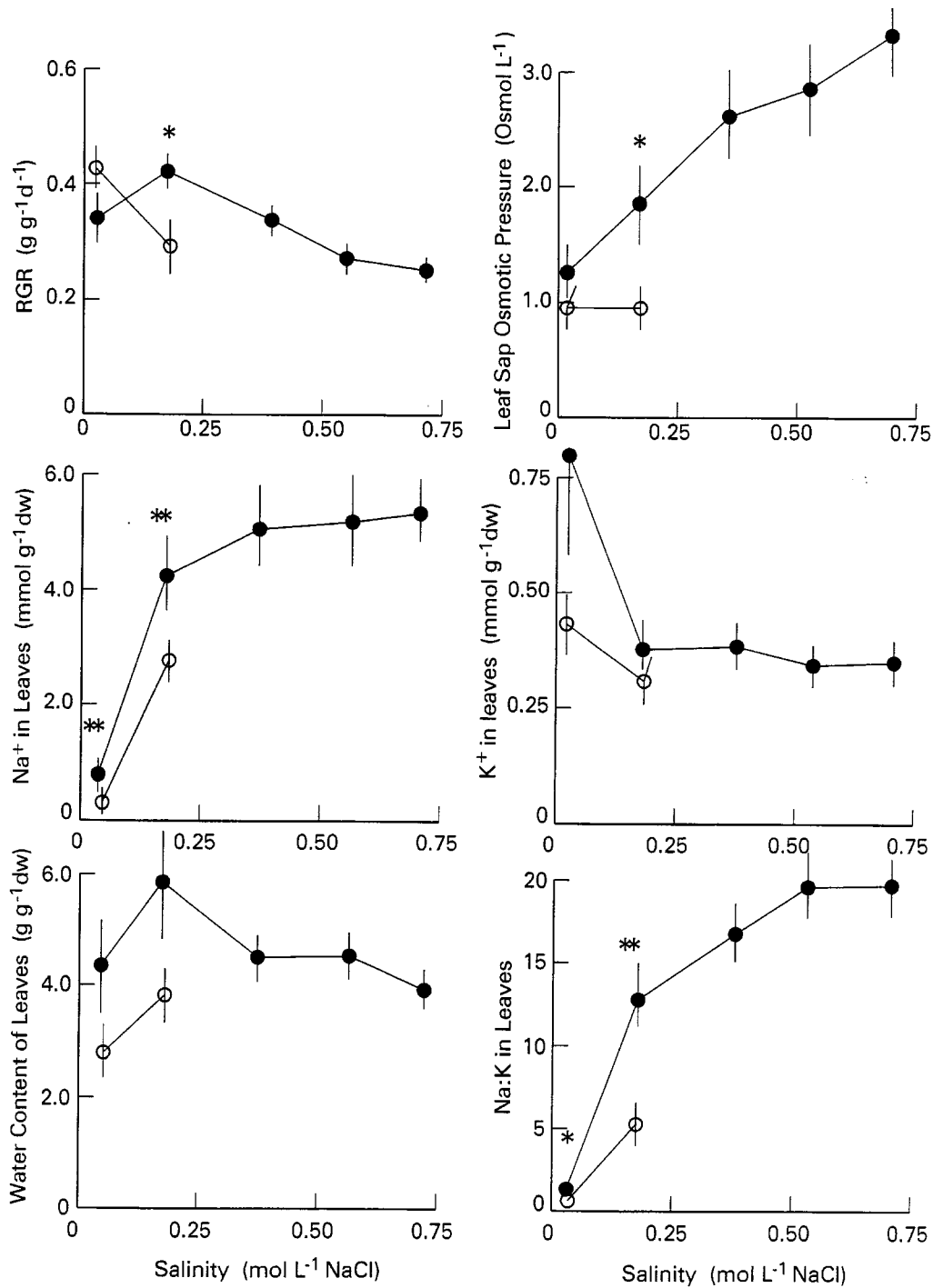


FIGURE 1. Growth of dicotyledonous halophytes and salt-tolerant glycophytes along a salinity gradient in a greenhouse screening experiment (Glenn and O'Leary, 1984). Ten species survived only to 0.18 mol/L NaCl (open circles = less tolerant species) whereas 10 others survived to 0.72 mol/L NaCl (closed circles = more tolerant species). Panels show relative growth rates (RGR); leaf osmotic pressure contributed by Na⁺, K⁺, and Cl⁻; and Na⁺, K⁺, water and Na:K content of leaves. Error bars are SE of means across species.

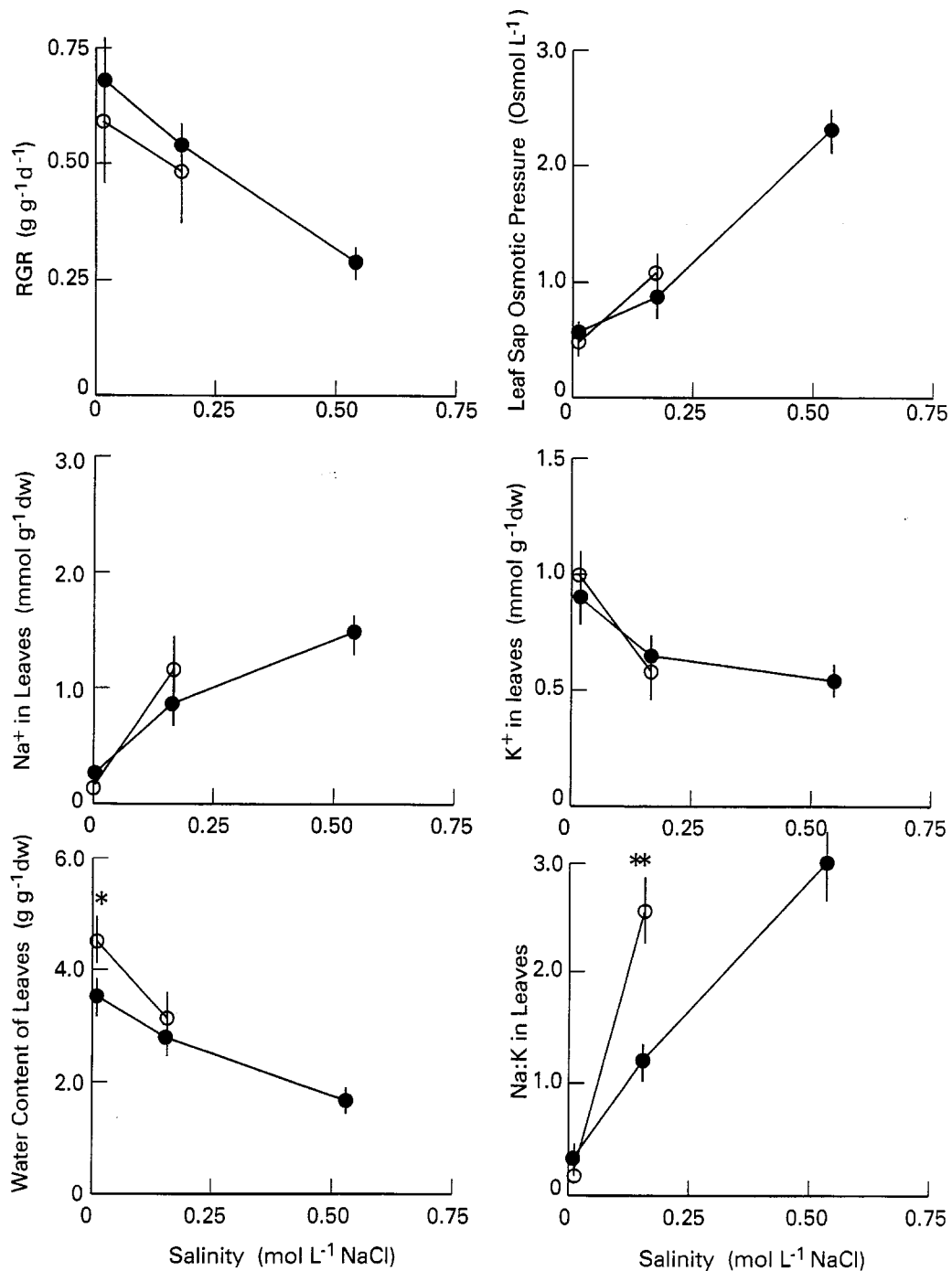


FIGURE 2. Growth of monocotyledonous halophytes and salt-tolerant glycophytes along a salinity gradient in a greenhouse screening experiment (Glenn, 1987). Fifteen species survived only to 0.18 mol/l NaCl (open circles = less tolerant species), whereas 12 others survived to 0.54 mol/l NaCl (closed circles = more tolerant species). Panels show relative growth rates (RGR); leaf osmotic pressure contributed by Na⁺, K⁺, and Cl⁻; and Na⁺, K⁺, water and Na:K content of leaves.

highly tolerant salt marsh plants such as *Spartina* and *Salicornia*. The species are pooled into two groups on each graph; those that had positive growth rates up to seawater salinity (540 mM NaCl or beyond) (= more tolerant) or those that had positive growth to 180 mM NaCl but did not survive on 540 mM NaCl (= less tolerant).

Growth of the more tolerant dicot halophytes was stimulated by 180 mM NaCl relative to controls, whereas less-tolerant dicots and all the grasses grew better on nonsalinized solution. This is not an absolute division because grasses and less-tolerant dicots may be stimulated by salinities lower than 180 mM NaCl (i.e., 25 to 100 mM NaCl) (Ungar, 1991). Although grasses were not stimulated by NaCl, the more tolerant grasses species grew as well as the more tolerant dicots on higher salt solutions. There was no inverse relationship between growth rate and salt tolerance; halophytes are not inherently slow-growing, as is sometimes assumed (Niu et al., 1995). The more tolerant dicot halophytes and both groups of grasses were osmoconformers, maintaining an osmotic pressure in the shoot approximately 2 to 3 times higher than the osmolality of the external solution. On the other hand, the less-tolerant dicots did not have the same ability to osmotically adjust. Na⁺K (times two to account for balancing anions) accounted for 80 to 95% of the cell sap osmotic pressure of both grasses and dicots at 180 mM NaCl and above, and Na⁺ was higher than K⁺ in shoot tissues of all plant on saline solutions, with the exception of sunflower (*Helianthus annuus*) (Glenn and O'Leary, 1984) and common reed (*Phragmites australis*) (Glenn, 1987), which excluded Na⁺ but did not survive above 180 mM NaCl. Thus, a (nearly) universal trait of salt-tolerant plants is the ability to accumulate NaCl for osmotic adjustment.

Comparative studies of halophyte species within a genus, for example, *Plantago* (Erdei and Kupier, 1979), or of genotypes within a species, such as *Atriplex canescens* (Glenn et al., 1992; 1994, 1996, 1997), *Armeria maritima*

(Koehl, 1997a,b), and *Salsola kali* (Reimman and Breckle, 1995), also show that halophyte salt tolerance can be positively correlated with capacity for Na⁺ uptake into the shoots. This relationship has been studied in detail in accessions of *A. canescens*, a xerohalophyte, adapted to both drought and salt stress. Growth rates on saline solutions differed among genotypes and was strongly ($r = 0.88^{***}$) correlated with capacity for Na⁺ accumulation ($n = 16$ accessions) and negatively ($r = -0.90^{***}$) correlated with capacity for K⁺ uptake (Glenn et al., 1996), the opposite of findings usually reported for halophytic grasses (Blits and Gallagher, 1991; Jeschke et al., 1995 — see also Figure 2). Differences in ion uptake capacity among genotypes were evaluated under nonsaline conditions prior to exposure of plants to a salinity gradient; hence, differences were not a consequence of salt treatment but were true predictors of performance.

C. Molecular and Genetic Determinants of Salt Tolerance

The most common view is that functional salt tolerance requires a series of integrated adaptations involving cellular systems, tissues and the whole plant (e.g., Cheeseman, 1988; Leach et al., 1990; Flowers and Yeo, 1995). Yet, some molecular biologists predict that just a few basic biochemical tolerance mechanisms, related through the effects of water-deficit and osmotic stress on cellular processes, may be sufficient to confer tolerance (Bohnert et al., 1995; Serrano, 1996; Serrano and Gaxiola, 1994; Zhu et al., 1997). They hypothesize that these mechanisms exist in glycophytes as well as halophytes but are more highly developed in adapted species. We test this viewpoint against what is known about specific tolerance mechanisms of halophytes, particularly those involved in ion homeostasis. The discussion centers on Na⁺, but in reality Cl⁻ is the common balancing anion for Na⁺, and it plays an equally important cellular role. Na⁺ has received the

most attention because of its inhibitory effect on enzyme activity and because it interferes with K^+ uptake and Ca^{2+} functions (in glycophytes), whereas Cl^- has received much less attention (Cheeseman, 1988).

It has been stated many times that halophyte cytoplasmic enzymes are not adapted to high salt levels, but there are differences between halophyte and glycophyte enzymes systems. For example, translation of wheat germ mRNA by polysomes extracted from leaves of halophytes (*Atriplex isatidea* and *Inula crithmoides*) had higher K^+ and Mg^{2+} optima than polysomes from glycophyte leaves (pea, wheat, rice, and barley), and Na^+ substituted for K^+ better in the halophyte than the glycophyte systems (Flowers and Dalmond, 1993). Interestingly, the extracellular (cell wall) enzymes of both glycophytes and halophytes are extremely salt tolerant (Thiyagarajah et al., 1996), suggesting that salt stress exerted through a high salinity in the apoplastic space may have been during the evolution of angiosperms.

Although the flux of Na^+ through the cytoplasm of halophyte cells might be high, the concentration of Na^+ in the cytoplasm is maintained at nontoxic levels (10 to 150 mM by different estimates) (Binzel et al., 1988; Cheeseman, 1988; Flowers et al., 1986; Fitzgerald et al., 1992) through the operation of ion translocases at the plasma membrane (to import Cl^- into the cell and to export Na^+ out of the cell) and tonoplast (to sequester Na^+ and Cl^- in the vacuole) (Barkla and Blumwald, 1991; Bennett and Spanswick, 1983; Blumwald and Poole, 1985a,b; Blumwald and Gelli, 1997; Churchill and Sze, 1984; Dupont, 1992; Niu et al., 1995; Pope and Leigh, 1987; Rausch et al., 1992; Serrano and Gaxiola, 1994; Zhu et al., 1997). Cell turgor is maintained by storage of NaCl in the cell vacuole, which contains 90% or more of cell water. The water potential in the cytoplasm of halophilic algae and higher plants is adjusted by the accumulation of organic solutes (Bohnert et al., 1995; Gorham et al., 1980; Koehl, 1997; Storey et al., 1977; Rhodes and Hanson, 1993), which may also function as

osmoprotectants, stabilizing membrane and enzyme structures and scavenging free radicals in a high osmotic environment (Bohnert et al., 1995).

This method of osmotic adjustment requires at least three types of adaptation with respect to ion homeostasis alone: (1) the capacity for controlled but rapid uptake of Na^+ and Cl^- into cells to support turgor-driven growth; (2) efficient sequestration of Na^+ and Cl^- into cell vacuoles; (3) and mechanisms to ameliorate the effects of excess entry of NaCl into the plant. In addition, halophytes require the ability to elaborate large quantities of compatible osmotica. We do not treat the role of organic solutes in the osmotic regulation of halophytes in detail here, but the subject has been reviewed by others (Rhodes and Hanson, 1993; Bohnert et al., 1995).

D. NaCl Uptake into Halophyte Cells

Surprisingly little is known about how Na^+ enters halophyte cells and tissues (Cheeseman, 1988). In glycophytes, two type of leakage are thought to be responsible for Na^+ entry into the plant. In some plants, such as rice, 20% or more of water entry into the plants is via transpirational bypass flow, by which water travels through the root in extracellular spaces rather than in the symplasm, and bypasses the endodermis to enter the transpiration stream directly (Garcia et al., 1997). If there is greater than about 50 mM NaCl in the external solution, enough Na^+ can be carried to the shoot via bypass flow to poison the leaves. In other plants, such as wheat, transpiration bypass flow is low (Garcia et al., 1997), but Na^+ leaks into the plant via the symplasm of root cortical cells by competitive binding onto K^+ transporters or cation channels (Rubio et al., 1995; Schachtman and Schroeder, 1994; Schachtman et al., 1991). This leakage not only allows damaging levels of Na^+ to enter the plant, but it depresses K^+ uptake. In plants growing at low salinity, internal Cl^- concentrations can exceed external concen-

trations by two orders of magnitude, and in general the Cl^- concentration in the plant appears to increase proportionally to the external supply (Flowers, 1988). Uptake of Cl^- appears to be mediated by the operation of a plasma membrane $\text{Cl}^-/2\text{H}^+$ symporter in *Chara* (a green alga) (Sanders, 1980) and perhaps also barley (Jacoby and Rudich, 1980).

These mechanisms do not seem plausible for halophytes, at least with respect to Na^+ entry. In the first place, halophytes often have thick layers of suberin or double layers of suberized cells at the root endodermis cells to prevent transpiration bypass flow (Anderson, 1974; Poljakoff-Mayber, 1974; Kramer, 1984). Direct measurements in *Aster tripolium* have shown virtually no penetration of NaCl past the root epidermis except by uptake into the symplasm (Zimmerman et al., 1992; see also Yeo and Flowers, 1986, for a discussion of Na^+ uptake by *Suaeda maritima*). Further, cellular Na^+ and K^+ uptake apparently are unlinked in halophytes, which maintain steady rates of K^+ uptake across wide ranges of external Na^+ and rate of Na^+ uptake (Flowers et al., 1977; Glenn and Brown, 1997; Glenn et al., 1996; Koehl, 1997a,b; Reimann, 1992; Reimann and Breckle, 1993, 1995) (see Figures 1 and 2). Hence, it is unlikely Na^+ leaks into halophyte cells via K^+ carriers.

Rates of Na^+ uptake into halophytes can be extremely high (Yeo and Flowers, 1986; Cheeseman, 1988). In succulent halophytes such as *Suaeda maritima* growing at 340 mM NaCl , Na^+ uptake by roots is 10 mmol/gdw/day, 10 times greater than K^+ uptake and probably too rapid for known carrier-transport processes (Yeo and Flowers, 1986). Active uptake may not be necessary because there is an electrochemical gradient of Na^+ across the cell membrane (Cheeseman, 1988). Uptake of Na^+ and Cl^- into halophyte cells may be via gated cation and anion channels, or even by vesicles (Cheeseman, 1988; Yeo and Flowers, 1986; Kurkova et al., 1992; Kurkova and Balnokin, 1994). Electron micrographs of four

halophytes growing on 400 mM NaCl showed pinocytotic invaginations on the cell membrane and vesicular bodies in the vacuoles, which were interpreted as evidence that ion transport from the apoplast to the vacuole in above-ground organs of salt-accumulating halophyte is carried out by means of pinocytosis (Kurkova and Balnokin, 1994).

E. Sequestration of NaCl Into Vacuoles

Na^+ must be actively pumped into the vacuole from the cytoplasm due to the low concentration in the cytoplasm, whereas Cl^- might enter passively via anion channels to balance electrical charge differences across the membrane (Blumwald, 1987; Dupont, 1992; Barkla et al., 1994; Rausch et al., 1996; Pantoja et al., 1990, 1992). Na^+ uptake into the vacuole appears to be mediated by Na^+/H^+ -antiporters in the tonoplast, working in concert with H^+ -ATPases and perhaps PP_i ases (Rea et al., 1992) that provide the proton motive force. Much more work has been done on the H^+ -ATPases, which have homology with enzymes from other organisms and therefore were easily cloned (Dupont, 1992), than with Na^+/H^+ -antiports, which have been cloned only recently (Apse et al., 1998; Darley et al., 1998).

Blumwald and Poole (1985a, 1987), working with red beet and sugar beet, were the first to describe antiporter activity in the tonoplast of salt-tolerant higher plants. Tonoplast antiporter activity has also been identified in roots or leaves of the halophytes *Atriplex nummularia* (Hassidim et al., 1990), *Plantago maritima* (Staal et al., 1991), *Atriplex gmelini* (Matoh et al., 1989), and *Mesembryanthemum crystallinum* (Barkla et al., 1995), as well as glyco-phytes such as barley (Garbarino and Dupont, 1988, 1989), cotton (Hassidim et al., 1990), and sunflower (Ballesteros et al., 1997). In some species, the vacuolar Na^+/H^+ antiport appeared to be constitutive, while in others the antiport was only activated by high NaCl concentrations. Increasing concentrations of NaCl in the

growth medium of sugar beet cell suspensions did not change the K_m but doubled the V_{max} of the antiport (Blumwald and Poole, 1987). An increase in V_{max} for the antiport with no change in apparent K_m suggested the addition of more antiport molecules to the tonoplast in response to NaCl in the growth medium.

A similar increase in Na^+/H^+ antiport activity has also been reported after the exposure of *Mesembryanthemum crystallinum* to high NaCl concentrations (Barkla et al., 1995; Low et al., 1996). Similar results were reported in sunflower roots (Ballesteros et al., 1997). In some salt-tolerant glycophytes, NaCl appears to activate preexisting tonoplast antiport molecules. In barley roots the operation of a tonoplast Na^+/H^+ antiport was demonstrated only when the roots were grown in the presence of NaCl (Garbarino and Dupont, 1988). The induction of the antiport activity by salt was very fast and appeared to be due to the activation of an existing protein rather than *de novo* synthesis, because the induction was observed in the presence of protein synthesis inhibitors (Garbarino and Dupont, 1989).

In *Plantago* species the vacuolar Na^+/H^+ antiport is present in the salt-tolerant *Plantago maritima*, but not in the more salt-sensitive *Plantago media* (Staal et al., 1991). The absence of Na^+/H^+ antiport activity in the tonoplast of *Plantago media* may be related to a general property observed in salt-sensitive plants (Mennen et al., 1990; Barkla et al., 1994). As a generality, in salt-tolerant glycophytes NaCl appears to activate pre-existing tonoplast antiport molecules, whereas in halophytes vacuolar antiports are constantly activated, even in plants grown in the absence of NaCl. This observation is consistent with the physiological data that show that halophytes rapidly scavenge Na^+ from the external medium and sequester it into the leaf cell vacuoles even at low external levels.

NaCl also induces V-type H^+ -ATPase activity in leaves of salt-treated plants (Ballesteros et al., 1996; Dupont, 1992; Kirsch et al., 1996; Low et al., 1996). Failure of V-type H^+ -

ATPase activity to respond to NaCl was cited as a cause of salt sensitivity in cotton seedlings (Lin et al., 1997); however, NaCl stimulated the enzyme most in mature rather than immature sugar beet leaves, which was interpreted as showing that rapidly growing tissues may already have maximal expression (Kirsch et al., 1996).

Cl^- plays an equally important role as Na^+ in osmoregulation and salt-tolerance (Flowers, 1988). In salt tolerant plants, Cl^- is compartmentalized in the vacuole in very high concentration (Matile, 1988). Fluctuations in cytoplasmic and vacuolar Cl^- concentrations have been shown to regulate the transport of other anions into the vacuole (Martinoia et al., 1987; Plant et al., 1994). The dissipation of a vacuolar positive membrane potential (generated by the activation of the vacuolar H^+ ATPase and H^+ pyrophosphatase) by anions revealed the existence of a uniport that allows Cl^- to accumulate in the vacuole in response to the membrane potential generated by the H^+ pumps (Bennett and Spanswick, 1983; Blumwald and Poole, 1985b; Kastner and Sze, 1987; Pope and Leigh, 1987). Dissipation of the membrane potential by Cl^- was saturable with a K_m of 2.3 mM (Kastner and Sze, 1987).

Tonoplast channels for passive ion movement of varying degrees of specificity are ubiquitous in plant cells, and several distinct types of channels involved in the transport of Cl^- have been identified (Hedrich and Nehr, 1987; Pantoja et al., 1992; Tyerman, 1992; Plant et al., 1994). The operation of these channels provides a uniport mechanism for the transport of Cl^- into the vacuole. Because the operation of the channel could also dissipate anion gradients established for active transport, one would expect the channel activity to be tightly controlled by factors such as membrane potential, Ca^{2+} and other ions. For example, intravacuolar Cl^- concentrations were shown to regulate the vacuolar anion channel activity; high vacuolar Cl^- concentrations favored the transport of nitrate and phosphate into the vacuole, and the influx of anions into the vacuole was coupled to Cl^-

efflux into the cytosol (Plant et al., 1994). In halophytes (and salt-tolerant glycophytes) cytoplasmic Cl^- concentrations have been estimated to be in the range of 25 to 150 mM (Cheeseman, 1988, Flowers et al., 1986). The concerted action of the two H^+ translocating pumps would generate a positive-inside vacuolar membrane potential of 40 to 80 mV (Blumwald, 1987), and this value could be underestimated if the salt-induced stimulation of the vacuolar H^+ ATPase is taken into consideration. Thus, vacuoles from salt-tolerant plants would be able to accumulate Cl^- at concentrations ranging from 200 to 1000 mM without expenditure of additional cellular energy.

F. Retention of NaCl in Halophyte Vacuoles

Once inside the vacuole, Na^+ is potentially susceptible to leakage back to the cytoplasm due to the steep concentration gradient between compartments; such leakage would increase the rate at which Na^+ would need to be pumped into the vacuole in the first place (Maathuis et al., 1992). Cl^- would leak only if the leakage of Na^+ proceeded to the point that the vacuole was no longer positively charged with respect to the cytoplasm. Vacuoles of high purity isolated from *Suaeda maritima* had highly saturated fatty acids and other lipid characteristics consistent with minimizing permeability to NaCl, but the protein content was low and the polypeptide content differed little from glycophyte tonoplast membranes (Leach et al., 1990). Furthermore, tonoplast cation channels through which Na^+ might leak back to the cytoplasm were found to be closed at physiological concentrations of Na^+ when measured in isolated *S. maritima* vacuoles by the patch-clamp technique (Maathuis et al., 1992). In the absence of leakage, a relatively small proportion of tonoplast H^+ ATPase activity would be needed to maintain NaCl compartmentation (10% in mature cells but more in expanding cells) (Maathuis et al., 1992). Hence, salt tolerance may not require

large expenditures of metabolic energy, raising the possibility that high yields are possible at high salinity.

G. Role of Plasma Membrane Anionports and ATPases

At the cellular level, halophytes and glycophytes can export Na^+ from the cytoplasm to the extracellular space via plasma-membrane Na^+/H^+ -anionports, with H^+ -ATPases operating at the plasmalemma providing the H^+ electrochemical gradient (Dupont, 1992; Niu et al., 1995). A series of studies on *Atriplex nummularia* showed evidence for a root plasmalemma anionporter that had higher activity in plants grown on 400 mM NaCl compared with controls, whereas cotton root plasmalemma anionporter activity was low and not affected by NaCl (Braun et al., 1986, 1988; Hassidim et al., 1990). The *A. nummularia* anionporter was not saturated by Na^+ up to 180 mM NaCl. NaCl also induced a P-type H^+ -ATPase from cell suspension cultures of *A. nummularia* that may supply energy for the anionporter, and up-regulation was also observed in roots and leaves of whole plants (Niu et al., 1993a,b, 1995). These studies support the hypothesis that halophytes are capable of expelling Na^+ from the cell.

The physiological function of these enzymes can be questioned because the rate of entry of NaCl into halophytes normally appears to be rate limiting for growth, and these enzymes would counteract NaCl uptake. A comparison of P-type H^+ -ATPase activity in salt-sensitive and salt-tolerance species of *Plantago* grown in the presence or absence of NaCl showed no differences between species or treatments and did not support a role for plasma membrane ATPases in regulating ion transport (Bruggemann and Jahiesch, 1987, 1988, 1989). A Na^+/H^+ anionporter was induced by salt in the tonoplast but not the plasma membrane of the salt-tolerant species (Staal et al., 1991). Other studies showed that the same type of NaCl stimulation of P- H^+ -ATPase occurred in the halophyte,

Salicornia bigelovii and a salt-sensitive cotton variety, suggesting that "...the activity of the PM-ATPase is not the primary determinant in salt tolerance and activity of the proteins on the plasma membrane alone may be insufficient to regulate intracellular Na⁺ levels" (Lin et al., 1997).

Clarification of the role of plasma membrane Na⁺/H⁺ antiporters and P-H⁺-ATPases has come from a detailed study of *A. nummularia* plants jumped suddenly to 400 mM NaCl (Niu et al., 1996). The salinity jump induced plasmolysis of cortical and endodermal root cells, presumably due to loss of water in response to NaCl accumulation in the apoplast; leaf mesophyll cells also showed ultrastructural changes, although they did not undergo plasmolysis. Apparently, the salt shock was mitigated in the root and not fully transferred to the shoot. Labeled RNA probes were infiltrated into fixed root and leaf tissues and showed the specific accumulation of mRNA for P-H-ATPase in root tip epidermal cells in the elongation zone (where first contact with Na⁺ occurs); in root endodermal cells in the elongation zone (where entry of Na⁺ into the stele is controlled); and in leaf bundle sheath cells (which are in direct contact with water transported to the leaf in the xylem). Plants on 200 mM NaCl did not show ultrastructural change or up-regulation of P-H-ATPase, and 7 days after transfer to 400 mM NaCl, cell structures of plants returned to normal appearance and mRNA for P-H-ATPase returned to barely detectable levels. Presumably, the P-H-ATPase levels were up-regulated to energize increased rates of secondary ion transport across the plasma membrane to control uptake of Na⁺ into cells and tissues during osmotic adjustment. Long-term adjustment apparently occurred through an increase in the resistance of the root cells to Na⁺ entry (mechanism unknown but presumably involving lower plasma membrane permeability to NaCl), and the plasmalemma Na⁺/H⁺ antiport system operated as a short-term mechanism to bale excess Na⁺ from the cell before such adjustment occurred. These molecular studies

support earlier physiological findings on the rapid adjustment of ion uptake by *Suaeda maritima* in response to salinity jumps (Clipson, 1996).

H. Ancillary Mechanisms of Salt Tolerance

In addition to the capacity to sequester NaCl in vacuoles and to produce compatible osmotica in the cytoplasm, halophytes have a diversity of secondary mechanisms to handle excess salt. At the tissue level, some halophytes have salt glands (Lipschitz and Waisel, 1982; Balsamo and Thomson, 1993, 1996), salt bladders (Schirmer and Breckle, 1982; Freitas and Breckle, 1992), or succulent tissues (Kramer, 1984; Yeo and Flowers, 1986) to handle temporary imbalances of NaCl entry into the plant. Although not all halophytes have salt excretion organs, in those that do 50% or more of the salt entering the leaf can be excreted (Bradley and Morris, 1991; Freitas and Breckle, 1992; Warwick and Halloran, 1992). Salt excretion, in turn, may perform secondary adaptive roles, such as light reflection from desert halophytes (e.g., *Atriplex*) (Osmond et al., 1980), or removal of excess salt from the root zone in salt marsh species such as *Spartina* (excreted salts are then carried away by the tides) (Bradley and Morris, 1991). Succulence can be a mechanism to dilute excess NaCl in the leaf tissues (Kramer, 1984), but the opposite phenomenon, reduction in leaf water content, is also commonly observed when halophytes are grown at high salinities; this concentrates NaCl in the cell sap, reducing the amount of NaCl that must be absorbed to support osmotic adjustment (Glenn and O'Leary, 1984; Glenn, 1987).

Halophytes can also increase their water use efficiency in response to salt, thereby minimizing the amount of water that must be transpired for each unit of growth (Guy et al., 1980; Guy and Reid, 1986; Ayala and O'Leary, 1995; Glenn et al., 1997). C₃ and C₄ species increase water use efficiency by lowering their stomatal

conductance in response to salt, which decreases rates of both photosynthesis and transpiration but not in direct proportion, resulting in an increase in water use efficiency (Osmond et al., 1980). Some facultative CAM plants, such as *Mesembryanthemum crystallinum*, switch from C_3 to CAM when exposed to salt, which also increases water use efficiency (e.g., Bohnert et al., 1995; Thomas and Bohnert, 1993); the switch to CAM is controlled by the growth stage of the plant and can be induced by other triggers such as low temperature, in addition to salinity (Ratajczak et al., 1994).

Nonhalophytes also increase water use efficiency in response to salt stress (Brugnoli and Bjorkman, 1992; Brugnoli and Lauteri, 1991; McCree, 1986; McCree and Richardson, 1987; Osmond et al., 1980; Shalhevet, 1993; Richards, 1992), and no unique adaptations of the photosynthetic apparatus have been identified in halophytes (e.g., Genard et al., 1991). However, a form of feedback control of stomatal opening by apoplastic Na^+ in the leaves has been identified in the halophyte, *Aster tripolium*, that has not been found in glycophytes (Perera et al., 1994, 1995, 1997).

I. Feasibility of Introducing Salt Tolerance into Glycophytes Through Gene Transfer: A Gedanken Experiment

Because conventional breeding to improve salt tolerance does not seem capable of yielding breakthrough advances, it is appropriate to ask whether direct transfer of halophyte genes into glycophytes might work. To our knowledge no experiments have been conducted, although glycophyte genes have been transferred into a halophyte through the gene gun technique (Li and Gallagher, 1996), so the question is open to speculation. The metabolic pathways to elaborate compatible osmotica appear to be present in all plants but may be blocked in glycophytes; hence, genetic manipulation of the promoter regions might induce these pathways in glycophytes (Bohnert et al., 1995). Could glycophytes then be induced to safely accumulate

$NaCl$ to support rapid growth and osmotic adjustment on salt solutions (the opposite target of conventional breeding programs that emphasize salt exclusion)?

Imagine a rice plant capable of producing organic solutes in the cytoplasm and with a halophyte-type Na^+/H^+ antiport system inserted into the tonoplast. Sufficient H^+ ATPase activity may already be present in glycophyte tonoplasts. The choice of rice is appropriate because $NaCl$ enters rice plants in the transpirational bypass flow at about the same rate as it is taken up by halophytes (Garcia et al., 1997; Yeo, 1994); furthermore, it is an aquatic plant, and halophytism is thought to have evolved first among coastal hydrophytes (Ungar, 1991). With the ability to sequester $NaCl$ into vacuoles, excess $NaCl$ would be absorbed into root and shoot cells in its passage through the plant, and it is conceivable that salt tolerance would be vastly improved by this single modification. However, Leach et al. (1990) regarded the capacity of the halophyte vacuole to retain Na^+ as an equally essential adaptation, and this appears to require alterations in the fatty acid profile of the membranes in addition to a functional Na^+/H^+ antiporter and H^+ -ATPases. Doubtless, there are many genes required for salt tolerance, but it will still be interesting to test the affect of single-gene additions or alterations on glycophytes, if the relevant halophyte genes can be cloned and transferred to glycophytes (Bohnert and Jensen, 1996). In the meantime, it may be possible to develop salt-tolerant crops through the direct domestication of halophytes.

IV. HALOPHYTES AS CROPS

The Israeli scientists Hugo and Elisabeth Boyko were the first modern researchers to attempt to develop high salinity agriculture (Boyko and Boyko, 1959; Boyko, 1966). They demonstrated that some crop plants could be grown on surprisingly high salinity in sandy soil, and pointed to the possibility of crossing crop plants such as wheat with salt-tolerant relatives such as *Agropyrum*, still a topic of

research interest. Growing plants in lysimeters made from empty oil drums on the Red Sea coast, they showed that a Bedouin strain of barley could complete its life cycle on full-strength seawater, presaging the findings of Epstein et al. (1980). While their experiments raised initial interest in high-salinity agriculture, their evidence tended to be anecdotal and there was no immediate follow-up by others. In fact, Boyko concluded (Boyko, 1966) that “Agrotechnical details for economic purposes have to be worked out...”, an understatement.

Interest revived in the 1970s, with some researchers working toward the development of salt-tolerant crops through breeding (Epstein et al., 1980) and others working on the domestication of wild halophytes (e.g., Somers, 1975; Felger, 1979), both approaches suggested by Boyko. A group at Scripps Institute of Technology conducted preliminary studies on seawater irrigation and compiled a list of potentially useful halophyte species (Mudie, 1974), which has been expanded (Aronson, 1989; National Research Council, 1990). Three research groups were initially responsible for most of the subsequent field trials of halophytes under irrigation: the Environmental Research Laboratory of the University of Arizona, USA (Glenn et al., 1996); the Halophyte Biotechnology Center, University of Delaware, USA (Gallagher, 1995); and the Institutes for Applied Research, Ben Gurion University of the Negev, Israel (Pasternak and Nerd, 1996; Pasternak and San Pietro, 1985). Malcolm (1996), working in Australia, and Le Houerou (1996), working in north Africa, have been most responsible for conducting field trials of halophytes under dryland conditions. Numerous other researchers at institutions throughout the arid zones are now considering halophyte trials (Squires and Ayoulo, 1994).

Four basic conditions must be met if halophytes are to succeed as irrigated crops: (1) they must have high yield potential; (2) the irrigation requirements must be within the range of conventional crops and must not damage the soil; (3) halophyte products must be able to substitute for conventional crop products; and (4) high-salinity agriculture must have a role to

play within the existing agricultural infrastructure. Whether halophytes can meet these conditions depends in part on their performance as agronomic crops, which in turn is related to their basic physiology and biochemistry in relation to salt stress.

A. Yield Potential of Halophytes

While there have been many laboratory studies carried out on the salt tolerance of halophytes, there have been relatively few field trials set up to simulate agronomic conditions. Ecological studies, however, have documented the high-yield potential of salt marsh species such as *Spartina alterniflora*, which produces up to 40 t/ha of biomass in the low intertidal zone of estuaries (Odum, 1974). Some halophytes complete their entire life cycles on beyond-seawater salinities (Troyo-Diequez et al., 1994).

Glenn and O’Leary (1985) reported yields ranging from 13.6 to 17.9 t/ha of dry matter for the most productive halophyte species in a screening of species carried out in field plots in a coastal desert environment (Puerto Penasco, Sonora, Mexico), using 40 g/l seawater as the irrigation source. These are comparable to yields obtained from conventional forage crops such as alfalfa or Sudan grass in desert irrigation districts. The native species outperformed the exotics, but the list of productive species included several plant types: a succulent, annual plant (*Salicornia bigelovii*); a perennial grass (*Distichlis palmeri*); a prostrate, rhizomatous plant with succulent leaves (*Batis maritima*); and several species of desert saltbush (*Atriplex* spp.).

Subsequent field trials at the same location confirmed the high-yield potential of halophytes irrigated with seawater. Over 6 years of field trials, the annual, oilseed halophyte *Salicornia bigelovii* produced 12.7 to 24.6 t/ha of biomass (mean = 18.0 t/ha) and 1.39 to 2.46 t/ha of seed (mean = 2.00 t/ha) over a 200-day growing cycle (Glenn et al., 1991). The seed contained 31% protein, 28% oil, and only 5% fiber and 5% ash; the oil was high in polyunsat-

urated fatty acids, particularly linoleic acid (74% of total).

Researchers at Ben Gurion University of the Negev tested 120 halophytes under full seawater irrigation (56 dS/m, approximately 34 g/l TDS) or on 15% seawater (5.5 dS/m) on the Mediterranean coast of Israel (Aronson et al., 1988). Seven *Atriplex* species produced 12.6 to 20.9 t/ha of biomass containing 9.9 to 19.5% protein on full-strength seawater, not significantly lower than the yields on 15% seawater. Gallagher (1985) obtained yields of 5.2 to 9.5 t/ha of the saltgrass *Distichlis spicata* under seawater (30 g/l) irrigation in Delaware, USA, while *Spartina patens* yielded 14.4 t/ha when harvested in July. These are within the range of yields from conventional forage grasses. The herbaceous plant *Atriplex triangularis*, a potential fresh vegetable crop for human consumption, yielded the equivalent of 21.2 t/ha on a fresh-weight basis. Zaruyk and Baalbaki (1996) proposed *Inula crithmoides*, a perennial halophyte bush, as a forage plant for saline irrigation. From small-scale experiments, they extrapolated a yield of 4 t/ha of dry biomass on 40 dS/m (24 g/l) seawater.

These reports show that halophytes can yield as high as conventional irrigated crops even under full seawater irrigation. However, the optimal salinity for growth of even the most tolerant halophytes is reportedly in the range 200 to 340 mM NaCl (11.4 to 19.4 g/l TDS) (Glenn and O'Leary, 1985; Yeo and Flowers, 1986). Hence, under high-salinity irrigation halophytes are beyond their growth optimum, and soil salt levels must be carefully controlled to avoid further yield reductions. This raises the question of whether high-salinity agriculture can ever be practical, even if adequate germplasm is developed.

B. Irrigation Requirements

Boyko believed that the key to irrigating with seawater was to use high volumes of water flooded onto very porous soils (Boyko and Boyko, 1966). In early experiments, Glenn and O'Leary (1985) used irrigation depths of 18

m/year to grow halophyte crops on seawater, simulating a tidal regime. This amount of water is greatly in excess of the amount of water applied to grow conventional crops on freshwater and is clearly uneconomical if the water must be pumped. More recent experiments have attempted to determine the minimum effective water requirement of halophytes on different salinities to determine the upper practical salinity limit for saltwater irrigation.

Miyamoto (1995) estimated the optimum soil salinity for several euhalophyte species grown under normal irrigation scheduling (allowing 50% soil moisture depletion between irrigations). The optimal salinity was approximately 20 g/l or less, and growth was observed to decline rapidly beyond soil salinities of 20 to 30 g/l. Because the salinity of the soil solution was 2 to 3 times as high as the salinity of the irrigation water, the irrigation water salinity optimum was about 10 g/l. They concluded that high-salinity water such as seawater required special measures to ensure the salinity of soil solution is maintained at levels that do not greatly inhibit plant growth.

This can be accomplished by leaching — applying sufficient water so that a portion of the applied water percolates past the plant root zone and carries with it excess salt applied in the irrigation water. The leaching fraction (LF) is the proportion of the applied water that percolates below the plant root zone (Ayers and Wescott (1985) and is given by the equation:

$$LF = \frac{\text{Depth of water leached below root zone}}{\text{Depth of water applied at the surface}}$$

The higher the leaching fraction, the lower the salinity of the soil water. However, higher leaching fractions and associated greater irrigation depths are associated with higher pumping cost and larger discharges of water to the aquifer or drainage system, which may be a problem where best management practices must be followed (e.g., Glenn et al., 1998). In general, there is no straight-forward rule to determine LF even for conventional crops. Ayers and

Wescott (1989) estimated the minimum Leaching Requirement (LR) as:

$$LR = EC_w / [5(EC_e) - EC_w]$$

where EC_w = salinity of the applied irrigation water in $dS\ m^{-1}$; EC_e = average soil salinity tolerated by the crop as measured on a soil saturation extract.

However, Miyamoto (1996) cautions that leaching requirements estimated by simple steady-state formulas may prove to be excessive with respect to handling drainage water when irrigating with seawater or high-salinity water that exceeds the optimum soil salinity for plant growth.

Glenn et al. (1997) irrigated *Salicornia bigelovii* over 2 years in drainage lysimeters set into a field of the same crop. The lysimeters were irrigated daily with seawater (40 g/l TDS) at five irrigation depths, ranging from 50 to 250% of the rate of evaporation from an evaporation pan. The application rates ranged from 0.73 to 3.79 m/year. Biomass yield increased in direct proportion to the water application rate, but all irrigation treatments produced a leaching fraction of about 0.35. Increasing the irrigation depth lowered the soil salinity, and resulted in higher plant growth and water use, and hence leaching fractions were approximately equal over all treatments. High yields required that the soil-moisture salinity be maintained below 75 g/l in the top 15 cm, which constitutes the root zone for this shallow-rooted species.

Consumptive water use by *S. bigelovii* was about the same as conventional biomass crops grown on freshwater in nearby irrigation districts (Figure 3). Hence, the “salt penalty” for growing crops on seawater is an additional 35% water requirement to handle excess salts. This may be a practical penalty to pay in locations with sandy coastal soils where seawater is the only large-scale water source that can be exploited for agriculture. The expense of pump-

ing water is directly proportional to the amount of lift required, and many irrigation districts use water from aquifers 100 m or deeper, whereas seawater along coastal deserts will usually require lifts of only 10 to 20 m. However, seawater irrigation also requires daily irrigation when soil with low water holding capacity (i.e., sand) is used; precision irrigation equipment, such as moving booms, must be used for water delivery, and these must be modified to handle seawater. A pilot-scale farm using four center-pivot booms, each irrigating 50 ha of *Salicornia bigelovii* with 44 g/l seawater, has been established in Saudi Arabia (Clark, 1994).

Much lower leaching fractions are possible if the salinity of the water is lower. Glenn et al. (1998) grew *Atriplex nummularia* in drainage lysimeters set in a closed-canopy plot of the same plant over 3 years in Tempe, Arizona, on water of 1.15 and 4.10 g/l TDS with no leaching fraction other than that provided by rainfall (7.4% of the irrigation volume). Although root zone, soil-moisture salinities ranged from 17.1 to 58.5 g/l in the lysimeters irrigated with the 4.1 g/l source, compared with only 2.2 to 5.1 g/l for the low-salinity source, the plants did not differ in growth rate and outperformed conventional crops in terms of both yield and water use efficiency (Figure 4). Hence, at least some halophyte crops grown at salinities above those that can be used on conventional crops but below the point where yield reductions occur deliver a bonus relative to conventional crops. Grieve and Suarez (1997) extrapolated yields of 7.4 t/ha per 3-week cutting interval from the halophyte *Portulaca oleracea* grown on approximately 12 g/l TDS water. These studies refute the notion that halophytes are inherently slow-growing plants (e.g., Niu et al., 1995).

C. Effect of High Salinity Water on the Soil

Another concern when irrigating with water with high sodium concentrations is that infiltration problems will result from soil

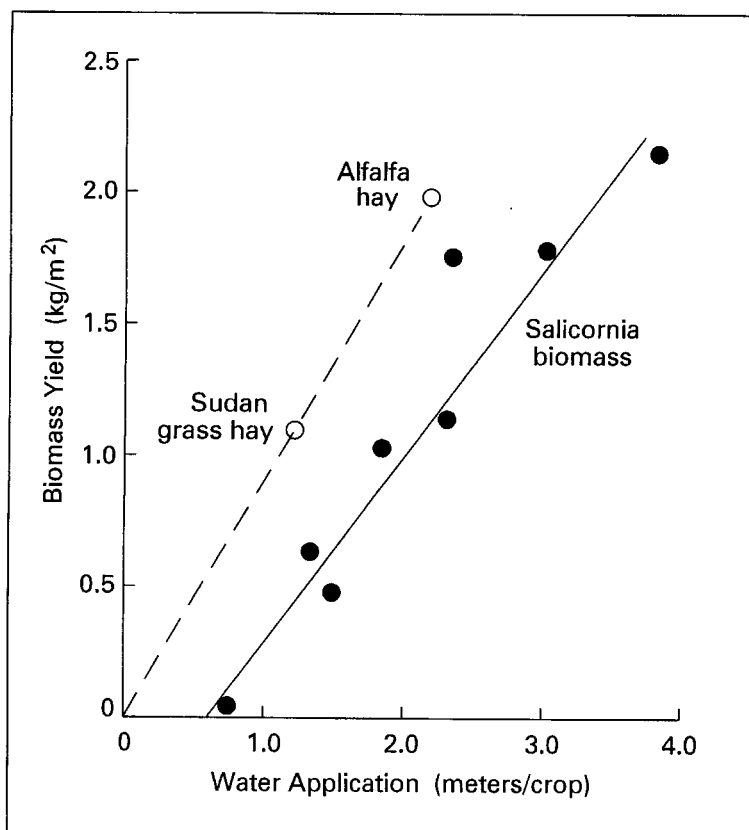


FIGURE 3. Biomass yield and irrigation requirements of *Salicornia bigelovii* irrigated with seawater (40 g/l TDS) in a coastal desert environment at Puerto Penasco, Sonora, Mexico, compared with conventional forage crops irrigated with fresh water in nearby irrigation districts in the United States (Glenn et al., 1997). Each data point is the mean value from four lysimeters. Data were collected over two growing seasons (four irrigation rates per growing season).

dispersion and structural breakdown. The sodium adsorption ratio (SAR) is the most commonly used method to assess potential infiltration problems. The SAR equation is

$$\text{SAR} = \text{Na}^+ / [\text{Ca}^{2+} + \text{Mg}^{+2}]$$

where concentrations are expressed in molar equivalents.

Generally, soils are classified as sodic when the $\text{SAR} > 15$, which would virtually preclude the use of high salinity water for irrigation. However, because the electrolyte concentration in seawater (and dilutions of seawater) is high relative to the sodium concentration, slow infiltration rates are generally not a

hazard for soil under seawater irrigation, even in susceptible soils (Quirk, 1971).

D. Useful Products from Halophytes

Although some halophytes are traditional human foods (Felger, 1979), most of the research has concentrated on their value in animal feeding systems. Animal feeds that can be produced from halophytes include forage from dried plant shoots (hay), oil, seed meal, and grains. Halophytes have mixed characteristics as forages. On the positive side, they generally have high protein content, ranging from 10 to 20% of dry matter (Le Houerou, 1996). On the negative side, they generally have high salt

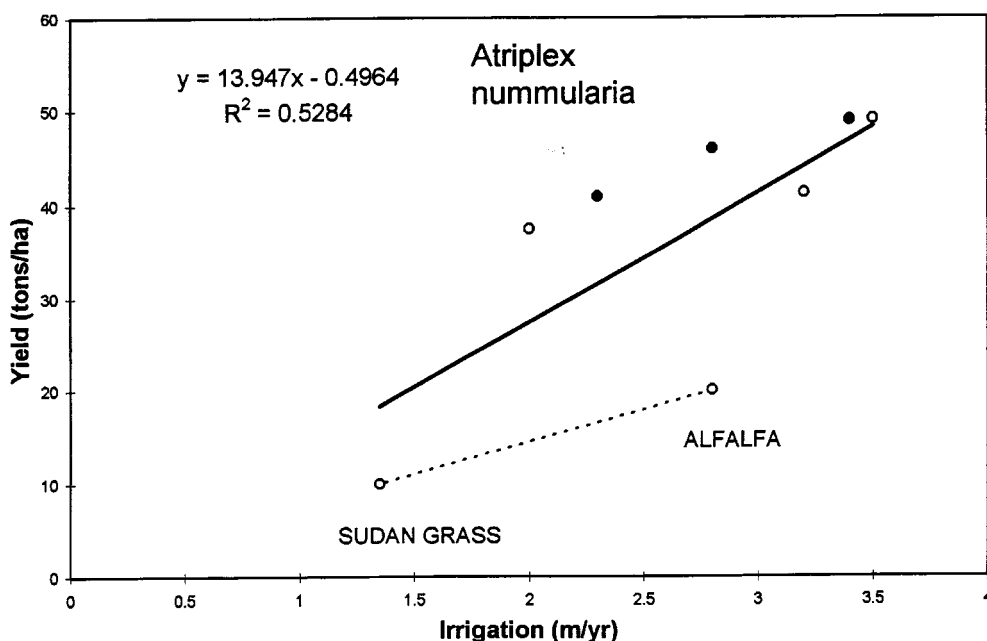


FIGURE 4. Biomass yield and irrigation requirements of *Atriplex nummularia* irrigated with 1 g/l (open circles) or 4 g/l (closed circles) industrial wastewater in Tempe, Arizona, compared with conventional forage crop yields and water use in nearby irrigation districts (Glenn et al., 1998). Each data point is the mean value over 3 years of data collection. The linear equation predicts yield (y) based on water use (x).

content (15 to 50% salts on the leaf dry matter) and are a fairly poor energy source (Le Houerou, 1996). Additionally, halophytes can occasionally contain oxalate levels in the toxic range (Le Houerou, 1996). While many halophyte species have been tested for use as forages, the salt bush genus *Atriplex* has received the most attention.

Atriplex species tend to have high protein content, generally ranging from 12 to 22% (Glenn et al., 1994; Watson, 1990). Crude protein of other halophyte species tends to be lower, and the protein content of *Salicornia bigelovii* straw ranges only from 4 to 6% (Glenn et al., 1995). However, in halophytes, estimates of crude protein overestimate the digestible protein content of the plant (O'Leary et al., 1985). This is because crude protein estimates may include non-protein nitrogen sources such as quaternary ammonia compounds and proline, which are used as osmocompatible sol-

utes by halophytes. Normally, these compounds, which can account for about 50% of the plant nitrogen content, are not digested and are excreted in the urine and the feces. However, Le Houerou (1996) has shown that it is possible for non-protein nitrogen to be metabolized when animals have been given sufficient time to develop rumen bacteria that are capable of using the non-protein nitrogen so long as there is sufficient energy in the diet to allow the bacteria to metabolize these compounds.

Despite all the aforementioned drawbacks associated with utilization of halophytes as forages, Swingle et al. (1996) demonstrated that halophytes could be incorporated into a practical lamb diet with no effect on growth performance. *Suaeda esteroa*, *Atriplex barclayana*, and *Salicornia bigelovii* straw were compared with conventional *Cynodon dactylon* hay (control) at 30% of the diet. All diets contained 12.5 to 15% protein and 50% grain as an energy

source, typical of high-performance fattening diets for ruminants. The halophyte forages contained a much higher ash content than the *Cynodon* hay (24 to 34% vs. 5%). Dry matter intake was higher for lambs fed diets containing halophytes forages than for lambs fed on the grass control diet. Lambs fed diets containing halophytes consumed more dry matter to compensate for the lower organic matter content of this diet compared with the control diet. Because of the increased intake, halophyte-fed lambs were able to gain at the same rate as the control lambs, but, as expected, the feed efficiency was lower and water intake was higher. Carcass quality of all lambs was excellent and was not affected by the inclusion of halophyte forages in the diet. Similar results were obtained with goats fed *Salicornia bigelovii* straw at up to 50% inclusion (Glenn et al., 1992). These results are in contrast to other results (Benjamin et al., 1992; Nerd and Pasternak, 1992) that reported poor utilization of *Atriplex barclayana* as a forage source for sheep at 70% inclusion. The key to effective utilization of salt-containing halophyte forage is to keep the forage component of the diet less than 50%, so the animals can compensate for the dilution effect that salt has on forage energy content by increasing their rate of intake (Swingle et al., 1996). Fattening diets generally contain 25 to 50% forage; hence, they appear to be the most practical feeding systems in which to use halophyte forages.

One of the most promising uses of halophytes may be as seed crops (Somers, 1975; Felger, 1979; O'Leary, 1988, 1994; Glenn et al., 1991; Jensen et al., 1988). One justification for this claim is that unlike the leaves that accumulate large amounts of salts, the seeds of halophytes have a very low salt content, even under saline irrigation. Halophyte seeds have been used as grains. *Distichlis palmeri* seeds were harvested by the Cocopa Indians of the Colorado River delta region (Felger, 1979; Jensen et al., 1988). Halophytes can also be grown for oilseed production. The perennial seashore mallow (*Kosteletzkya virginica*) produces a seed that is 32% protein and 22% lipid (Gal-

lagher, 1985; Poljakoff-Mayber et al., 1994). Glenn et al. (1991) examined the oil of *Salicornia bigelovii* seeds and found it similar in caloric value to soybean oil. No difference in growth rate was found in chickens fed a diet containing soybean oil at 2% of the total diet as an energy supplement, and chickens fed a diet where the soybean oil was replaced by *S. bigelovii* oil at 2% of the diet. However, there was growth inhibition of chickens fed the *S. bigelovii* seed meal at 10% or greater inclusion. It is believed that the growth depression was caused by saponins. Growth inhibition was reversed when the *S. bigelovii* seed meal was supplemented with cholesterol at 1%, as cholesterol counteracts the antigrowth properties of saponins. Similar results were found by Attia et al. (1997). Ruminants are less susceptible to saponins than poultry, and seed meal from *S. bigelovii* was able to replace cottonseed meal as a protein supplement (10% inclusion rate) with no effect on animal performance.

E. Role of High-Salinity Tolerant Crops in Agriculture

The prospect of greening the world's coastal deserts with seawater crops has been the most cited scenario for highly tolerant crops, but there are more immediate opportunities for high-salinity agriculture. There is currently a need to develop highly salt-tolerant crops to recycle agricultural drainage water, literally rivers of contaminated water that are generated in arid-zone irrigation districts. This water can become an environmental hazard when discharged into surface waters or placed in evaporation ponds, through the evapoconcentration and bioaccumulation of toxic elements (Boyle, 1996; Hothem and Ohlendorf, 1989; Matsui et al., 1992; Ong and Tanji, 1993; Ong et al., 1995; Presser, 1994). Perhaps the best solution is to reuse the water near the site of production on progressively more salt-tolerant crops, thereby reducing the amount of water that must ultimately be disposed (Grieve and Suarez, 1997; Rhoades, 1993; Rhoades et al.,

1989; Wescott, 1988). A limitation to the reuse of such water is the low salt tolerance of the conventional crops (Rhoades et al., 1989; Wescott, 1988) and trees (Karajeh et al., 1994; Karajeh and Tanji, 1994a,b) that have been tested as secondary crops. Halophytes could greatly extend the range of options for disposing of this type of salty water (Riley et al., 1998; Glenn et al., 1998; Watson and O'Leary, 1993; Watson et al., 1994; Grieve and Suarez, 1997). Another use for halophyte crops is to reclaim saline soils (Keiffer and Ungar, 1997a,b). Through their capacity for salt uptake, halophyte can reduce the salt content of soil over time (as long as they are not irrigated with saline water).

Worldwide, approximately 45 to 60 million ha of irrigated land have been damaged by salt, representing 20 to 25% of the total irrigated acreage in the world (Ghassemi et al., 1995). Reclaiming these lands for conventional crops is too costly for most countries to afford, but they could be used to grow halophytes, as is being attempted in Pakistan, as an example (Quereshi et al., 1991). As salt marsh plants, many halophytes are not only salt tolerant but can thrive in poorly drained soils, which are the first to become salinized in irrigation districts. It is sometimes argued that, in the absence of complete reclamation, halophyte crops could only postpone the inevitable salting up of such land (but this would be a benefit by itself). A counterargument is that marginal land can be used for sustained halophyte production in circumstances where unrealistic inputs would be needed to maintain soil salt levels low enough for conventional crops.

CONCLUSIONS

Halophytes are a diverse group of plants with varying degrees of actual salt tolerance, yet they appear to share in common the ability to sequester NaCl in cell vacuoles as the major plant osmoticum. This requires at a minimum a

functional Na^+/H^+ antiport system in the tonoplast and perhaps special membrane properties to avoid leakage of Na^+ from the vacuole to the cytoplasm. They also must accumulate organic solutes in the cytoplasm to balance the osmotic potential in the vacuole. The emerging evidence points to specialized properties of halophyte ion transporters compared with glycophyte enzymes, which allow them to take up and sequester NaCl with high efficiency. Halophyte membrane lipids may also be adapted to prevent salt leakage.

Although NaCl inhibits the growth even of halophytes at levels approaching seawater salinity, the metabolic cost of salt tolerance is not so high that plants are unproductive at high salinity. Halophytes grown on seawater can produce high yields of seed and biomass, and the irrigation requirements are within the range of conventional crops. When grown at lower salinities, C_4 halophytes such as *Atriplex nummularia* can substantially outperform conventional crops in yield and water use efficiency.

Current efforts to produce salt-tolerant conventional crops are aimed mainly at increasing the salt-exclusion capacity of glycophytes. However, these efforts have not produced breakthroughs in salt tolerance (Flowers and Yeo, 1995), as was predicted twenty years ago (Epstein et al., 1980). Research with halophytes, by contrast, have identified several prospective crop species and have demonstrated the overall feasibility of high-salinity agriculture, given suitable germplasm. Progress in producing highly tolerant cultivars of conventional crops may require a change in strategy, to attempt to introduce halophyte genes directly into glycophytes (Bohnert and Jensen, 1996). Such research has not even begun, but the tools are at least being assembled, including an understanding of the molecular determinants of halophyte salt tolerance. In the meantime, the quickest way forward may be the direct domestication of halophytes, which have already been used to demonstrate the feasibility of high-salinity agriculture.

REFERENCES

- Ahmad, I., Larher, F., and Stewart, G. 1981a. The accumulation of acetylornithine and other solutes in the salt marsh grass *Puccinellia maritima*. *Phytochemistry*. **20**:1501–1504.
- Ahmad, I., Wainright, S., and Stewart, G. 1981b. The solute and water relations of *Agrostis stolonifera* ecotypes differing in their salt tolerance. *New Phytol.* **87**:615–629.
- Albert, R. and Popp, M. 1977. Chemical composition of halophytes from the Neusiedler Lake region in Austria. *Oecologia* **27**:157–170.
- Anderson, C. 1974. A review of structure in several North Carolina salt marsh plants. **In: Ecology of Halophytes.** pp. 307–344. Reimold, R. and Queen, W., Eds., Academic Press, New York.
- Apse, M. P., Aharon, G. S., Snedden, W. A., and Blumwald, E. 1998. Cloning and characterization of plant sodium/proton antiports. *Proceedings of the 11th International Workshop on Plant Membrane Biology.* Cambridge, UK, pp. 84.
- Aronson, J. A. 1989. *HALOPH: A Data Base of Salt Tolerant Plants of the World.* Arid Land Studies, University of Arizona, Tucson, AZ.
- Aronson, J. A., Pasternak, D., and Danon, A. 1988. Introduction and first evaluation of 120 halophytes under seawater irrigation. **In: Arid Lands Today and Tomorrow: Proceedings of an International Research and Development Conference.** pp. 737–746. Whitehead, E. E., Hutchinson, C. F., Timmerman, B. N., and Varady, R. G., Eds., Westview Press, Boulder, CO.
- Ashraf, M. 1994. Breeding for salinity tolerance in plants. *CRC Crit. Rev. Plant. Sci.* **13**:17–42.
- Asins, M. J., Breto, M. P., Cambra, M., and Carbonell, E. A. 1993. Salt tolerance in *Lycopersicon* species. I. Character definition and changes in gene expression. *Theor. Appl. Genet.* **86**:737–743.
- Attia, F., Alsobayel, A., Kriadees, M., Al-Saiady, M., and Bayoumi, M. 1997. Nutrient composition and feeding value of *Salicornia bigelovii* Torr. meal in broiler diets. *Anim. Feed Sci. Technol.* **65**: 257–263.
- Ayala, F. and O’Leary, J. 1995. Growth and physiology of *Salicornia bigelovii* Torr. at suboptimal salinity. *Int. J. Plant Sci.* **156**:197–205.
- Ayala, F., O’Leary, J., and Schumaker, K. 1996. Increased vacuolar and plasma membrane H⁺-ATPase activities in *Salicornia bigelovii* Torr. in response to NaCl. *J. Exp. Bot.* **47**:25–32.
- Ayers, R. S. and Wescott, D. W. 1989. Water quality for agriculture. *FAO Irrig. Drain. Paper* **29**:737–746.
- Ballesteros, E., Blumwald, E., Donaire, J., and Belver, A. 1997. Na⁺/H⁺ antiport activity in tonoplast vesicles isolated from sunflower roots induced by NaCl stress. *Physiol. Plant.* **99**:328–334.
- Ballesteros, E., Donaire, J., and Belver, A. 1996. Effects of salt stress on H⁺-ATPase and H⁺PPase activities of tonoplast-enriched vesicles isolated from sunflower roots as affected by salt stress. *Physiol. Plant.* **97**:259–268.
- Balsamo, R. and Thomson, W. 1996. Isolation of mesophyll and secretory cell protoplasts of the halophyte *Ceratostigma plumbaginoides* (L.): a comparison of ATPase concentration and activity. *Plant Cell Rep.* **15**:418–422.
- Balsamo, R. and Thomson, W. W. 1993. Ultrastructural features associated with secretion in the salt glands of *Frankenia grandifolia* (Frankeniaceae) and *Avicennia germinans* (Avicenniaceae). *Am. J. Bot.* **80**:1276–1283.
- Barkla, B., Apse, M. P., Manolson, M. F., and Blumwald, E. 1994. The plant vacuolar Na⁺/H⁺ antiport. **In: Membrane Transport in Plants and Fungi: Molecular Mechanisms and Control.** pp. 141–153. Blatt, M., Leigh, R., and Sanders, D., Eds., SEB, London.
- Barkla, B. and Blumwald, E. 1991. Identification of a 170-kDa protein associated with the vacuolar Na⁺/H⁺ antiport of *Beta vulgaris*. *Proc. Nat. Acad. Sci. U.S.A.* **88**:11177–11181.
- Barkla, B., Zingarelli, L., Blumwald, L., and Smith, J. 1995. Tonoplast Na⁺/H⁺ antiport activity and its energization by the vacuolar H⁺-ATPase in the halophytic plant *Mesembryanthemum crystallinum*. *Plant Physiol.* **108**:549–556.
- Benjamin, R., Oren, E., Katz, E., and Becker, K. 1992. The apparent digestibility of *Atriplex barclayana* and its effect on nitrogen balance in sheep. *Anim. Prod.* **54**:259–264.
- Bennett, A. and Spanswick, R. 1983. Optical measurements of delta-pH and delta-water potential in corn root membrane vesicles. Kinetic analysis of

- Cl⁻ effects on a proton translocating ATPase. *J. Membr. Biol.* **71**:95–107.
- Binzel, M., Hess, F., Bressen, R., and Hasegawa, P. 1988. Intracellular compartmentation of ions in salt-adapted tobacco cells. *Plant Physiol.* **86**: 607–614.
- Blits, K. and Gallagher, J. 1991. Morphological and physiological responses to increased salinity in marsh and dune ecotypes of *Sporobolus virginicus* (L.) Kunth. *Oecologia* **87**:330–335.
- Blumwald, E. 1987. Tonoplast vesicles as a tool in the study of ion transport at the plant vacuole. *Physiol. Plant.* **69**:731–734.
- Blumwald, E., Cragoe, E., and Poole, R. 1987b. Inhibition of Na⁺/H⁺ antiport activity in sugar beet tonoplast by analogs of amiloride. *Plant Physiol.* **85**:30–33.
- Blumwald, E. and Gelli, A. 1997. Secondary inorganic ion transport at the tonoplast. *Adv. Bot. Res.* **25**:401–407.
- Blumwald, E. and Poole, R. 1985a. Na⁺/H⁺-antiport in isolated tonoplast vesicles from storage tissue of *Beta vulgaris*. *Plant Physiol.* **78**:163–167.
- Blumwald, E. and Poole, R. 1985b. Nitrate storage and retrieval in *Beta vulgaris*: effects of nitrate and chloride on proton gradients in tonoplast vesicles. *Proc. Natl. Acad. Sci. U.S.A.* **82**:3683–3687.
- Blumwald, E. and Poole, R. 1987. Salt-tolerance in suspension cultures of sugar beet. I. Induction of Na⁺/H⁺-antiport activity at the tonoplast by growth in salt. *Plant Physiol.* **83**:884–887.
- Blumwald, E., Rea, P., and Poole, R. 1987d. Preparation of tonoplast vesicles: applications to H⁺-coupled secondary transport in plant vacuoles. *Methods Enzymol.* **148**:115–123.
- Bohnert, H. and Jensen, R. 1996. Metabolic engineering for increased salt tolerance — the next step (with reply by T. Flowers and A. Yeo). *Aust. J. Plant Physiol.* **23**:661–667.
- Bohnert, H., Nelson, D. E., and Jensen, R. G. 1995. Adaptations to environmental stresses. *Plant Cell* **7**:1099–1111.
- Boyko, H. and Boyko, E. 1959. Seawater irrigation, a new line of research on a bioclimatic plant-soil complex. *Int. J. Bioclim.* **3**:1–17.
- Boyko, H. 1966. *Salinity and Aridity: New Approaches to Old Problems*. Dr. W. Junk, The Hague.
- Boyle, R. 1996. Life, or death, for the Salton Sea (the plight of California's otherworldly sea). *Smith.* **27**:86–96.
- Bradley, P. M. and Morris, J. T. 1991. Relative importance of ion exclusion, secretion and accumulation in *Spartina alterniflora* Loisel. *J. Exp. Bot.* **42**:1525–1532.
- Braun, Y., Hassidim, M., Lerner, H., and Reinhold, L. 1988. Evidence for a Na⁺/H⁺ antiporter in membrane vesicles isolated from roots of the halophyte *Atriplex nummularia*. *Plant Physiol.* **87**:104–108.
- Braun, Y., Hassidim, M., Lerner, H., and Reinhold, L. 1986. Studies on H⁺-translocating ATPases in planting of varying resistance to salinity. I. Salinity during growth modulates the proton pump in the halophyte *Atriplex nummularia*. *Plant Physiol.* **81**:1050–1056.
- Bruggemann, W. and Janiesch, P. 1987. Comparison of plasma membrane H⁺-ATPase from salt-tolerant and salt-sensitive *Plantago* species. *J. Plant Physiol.* **130**:395–411.
- Bruggemann, W. and Jahiesch, P. 1988. Properties of native and solubilized plasma membrane ATPase from the halophyte *Plantago crassifolia* grown under saline and non-saline conditions. *Physiol. Plant.* **74**:615–622.
- Bruggemann, W. and Jahiesch, P. 1989. Comparison of plasma membrane ATPase from salt-treated and salt-free grown *Plantago maritima* L. *J. Plant Physiol.* **134**:20–25.
- Brugnoli, E. and Bjorkman, O. 1992. Growth of cotton under continuous salinity stress: influence on allocation pattern, stomatal conductance and non-stomatal components of photosynthesis and dissipation of excess light energy. *PLANA* **187**:335–347.
- Brugnoli, E. and Lauteri, M. 1991. Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C₃ non-halophytes. *Plant Physiol.* **95**:628–635.
- Cheeseman, J. 1988. Mechanisms of salinity tolerance in plants. *Plant Physiol.* **87**:104–108.
- Choukr-Allah, R., Malcolm, C. V., and Hamdy, A. 1996. *Halophytes and Biosaline Agriculture*. Marcel Dekker, New York.
- Churchill, K. and Sze, S. 1984. Anion-sensitive H⁺-pumping ATPase of oat roots: direct effects of

- Cl⁻, NO₃⁻ and disulfonic stilbene. *Plant Physiol.* **83**:884–887.
- Clark, A. 1994. Samphire: from sea to shining seed. *Aramco W.* **45**:2–9.
- Clipson, N. 1987. Salt tolerance in the halophyte *Suaeda maritima* L. Dum. Growth and ion exchange in response to altered salinity. *J. Exp. Bot.* **38**:1996–2004.
- Darley, C. P., van Wuyt Swinkel, D., van der Woude, K., Mager, P., and de Goer, B. 1998. ANA1a Na⁺/H⁺ antiport from *Arabidopsis*? *Proceedings of the International Workshop on Plant Membrane Biology*. Cambridge, UK, pp. 8.
- Dupont, F. 1992. Salt-induced changes in ion transport: regulation of primary pumps and secondary transporters. **In:** *Transport and Receptor Proteins of Plant Membranes*. pp. 91–100. Cooke, D. and Clarkson, D., Eds., Plenum Press, New York.
- Dvorak, J., Noaman, M., Goyal, S., and Gorham, J. 1994. Enhancement of the salt tolerance of *Triticum turginum* L. by the Kna1 locus from the *Triticum aestivum* L. chromosome 4D by homoeologous recombination. *Theoret. Appl. Genet.* **87**:872–877.
- Epstein, E., Norlyn, J., Rush, D., Kingsbury, R., Kelley, D., Cunningham, G., and Wrona, A. 1980. Saline culture of crops: a genetic approach. *Science* **210**:399–404.
- Erdei, L. and Kuiper, P. 1979. The effect of salinity on growth, cation content, Na⁺-uptake and translocation in salt-sensitive and salt-tolerant *Plantago* species. *Physiol Plant.* **47**:95–99.
- Felger, R. S. 1979. Ancient crops for the twenty-first century. **In:** *New Agricultural Crops*. pp. 5–20. Ritchie, G. A., Ed., Westview Press, Boulder, CO.
- Fitzgerald, M. A., Orlovich, D. A., and Allaway, W. G. 1992. Evidence that abaxial leaf glands are the sites of salt secretion in leaves of the mangrove *Avicennia marina* (Forsk.) Vierh. *New Phytol.* **120**:1–7.
- Flowers, T. J. 1988. Chloride as a nutrient and as an osmoticum. **In:** *Advances in Plant Nutrition*. Vol. 3. pp. 55–78. Tinker, B. and Lauchii, A., Eds., Praeger, New York.
- Flowers, T. and Dalmond, D. 1993. Protein synthesis in halophytes: the influence of potassium, sodium and magnesium in vitro. *Dev. Plant Soil Sci.* **50**:195–203.
- Flowers, T., Troke, P. F., and Yeo, A. R. 1977. The mechanism of salt tolerance in halophytes. *Ann. Rev. Plant Physiol.* **28**:89–121.
- Flowers, T. and Yeo, A. 1986. Ion relations of plants under drought and salinity. *Aust. J. Plant Physiol.* **13**:75–91.
- Flowers, T. and Yeo, A. 1988. Ion relations of salt tolerance. **In:** *Solute Transport in Plant Cells and Tissues*. pp. 392–416. Baker, D. and Halls, J., Eds., Longman, London.
- Flowers, T. and Yeo, A. 1995. Breeding for salinity resistance in crop plants: where next? *Aust. J. Plant Physiol.* **22**:875–884.
- Freitas, H. and Breckle, S. 1992. Importance of bladder hairs for salt tolerance of field-grown, *Atriplex* species from a Portuguese salt marsh. *Flora Morphol. Geobot. Oekophysiol.* **187**:283–297.
- Fricke, W., Leigh, R. A., and Tomos, A. D. 1996. The intercellular distribution of vacuolar solutes in the epidermis and mesophyll of barley leaves changes in response to NaCl. *J. Exp. Bot.* **47**:1413–1426.
- Gallagher, J. L. 1985. Halophytic crops for cultivation at seawater salinity. *PLSOA* **89**:323–336.
- Garbarino, J. and Dupont, F. 1988. NaCl induces a Na⁺/H⁺ antiport in tonoplast vesicles from barley roots. *Plant Physiol.* **86**:231–236.
- Garbarino, J. and Dupont, F. 1989. Rapid induction of Na⁺/H⁺ exchange activity in barley root tonoplasts. *Plant Physiol.* **86**:231–236.
- Garcia, A., Rizzo, C., Ud-Din, J., Bartos, S., Senadhira, D., Flowers, T., and Yeo, A. 1997. Sodium and potassium transport to the xylem are inherited independently in rice, and the mechanism of sodium: potassium selectivity differs between rice and wheat. *Plant Cell Environ.* **20**:1167–1174.
- Garrill, A., Tyerman, S. D., and Findlay, G. P. 1994. Ion channels in the plasma membrane of protoplasts from the halophytic angiosperm *Zostera muelleri*. *J. Membr. Bio.* **142**:381–393.
- Genard, H., le Saos, J., Billard, J. P., Tremolieres, A., and Boucaud, J. 1991. Effect of salinity on lipid composition, glycine betaine content and photosynthetic activity in chloroplasts of *Suaeda maritima*. *Plant Physiol. Biochem.* **29**:421–428.
- Ghassemi, F., Jakeman, A., and Nix, H. 1995. *Salinization of Land and Water Resources: Human Causes, Extent, Management and Case Studies*. University of South Wales Press, Sydney, Australia.

- Glenn, E. P. 1987. Relationship between cation accumulation and water content of salt tolerant grasses and a sedge. *Plant Cell Environ.* **10**:205–212.
- Glenn, E. and Brown, J. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in drying soil. *Am. J. Bot.* **85**:10–16.
- Glenn, E. P., Coates, W., Riley, J. J., Kuehl, R., and Swingle, R. S. 1992. *Salicornia bigelovii* Torr.: a seawater-irrigated forage for goats. *Anim. Feed Sci. Technol.* **40**:21–30.
- Glenn, E., Hicks, N., Riley, J., and Swingle, R. 1996. Seawater irrigation of halophytes for animal feed. **In:** *Halophytes and Biosaline Agriculture*. pp. 221–236. Chakour-Allah, R., Malcolm, C.V., and Hamdy, A., Eds., Marcel Dekker, New York.
- Glenn, E., Miyamoto, M., Moore, D., Brown, J. J., Thompson, T. L., and Brown, P., 1997. Water requirements for cultivating *Salicornia bigelovii* Torr. with seawater on sand in a coastal desert environment. *J. Arid Environ.* **36**:711–730.
- Glenn, E. P. and O’Leary, J. 1984. Relationship between salt accumulation and water content of dicotyledonous halophytes. *Plant Cell Environ.* **7**:253–261.
- Glenn, E. P. and O’Leary, J. 1985. Productivity and irrigation requirements of halophytes grown with seawater in the Sonoran Desert. *J. Arid Environ.* **9**:81–91.
- Glenn, E. P., O’Leary, J. W., Watson, M. C., Thompson, T. L., and Kuehl, R. O. 1991. *Salicornia bigelovii* Torr.: an oilseed halophyte for seawater irrigation. *Science* **251**:1065–1067.
- Glenn, E. P., Olsen, M., Frye, R., Moore, D., and Miyamoto, M. 1994. How much sodium accumulation is necessary for salt tolerance in subspecies of the halophyte, *Atriplex canescens*? *Plant Cell Environ.* **17**:711–719.
- Glenn, E. P., Pfister, R., Brown, J., Thompson, T. L., and O’Leary, J. 1996. Na and K accumulation and salt tolerance of *Atriplex canescens* (Chenopodiaceae) genotypes. *Am. J. Bot.* **83**:997–1005.
- Glenn, E., Tanner, R., Miyamoto, M., Fitzsimmons, K., and Boyer, J. 1998. Water use productivity and forage quality of the halophyte *Atriplex nummularia* grown on saline waste water in a desert environment. *J. Arid Environ.* **38**:45–62.
- Glenn, E. P., Watson, M. C., and O’Leary, J. W. 1992b. Comparison of salt tolerance and osmotic adjustment of low-sodium and high-sodium subspecies of the halophyte, *Atriplex canescens*. *Plant Cell Environ.* **15**:711–718.
- Gorham, J., Hughes, L., and Wyn Jones, R. 1980. Chemical composition of salt-marsh plants from Ynys Mon (Anglesey): the concept of physiotypes. *Plant Cell Environ.* **3**:309–318.
- Gorham, J. and Wyn Jones, R. 1993. Utilization of Triceae for improving salt tolerance in wheat. **In:** *Towards the Rational Use of High Salinity Tolerant Plants*, Vol. 2. pp. 27–34. Lieth, H. and Maasoom, A., Eds., Kluwer, Dordrecht.
- Greenway, H. 1968. Growth stimulation by high chloride concentrations in halophytes. *Isr. J. Bot.* **17**:169–177.
- Greenway, H. and Munns, R. 1980. Mechanisms of salt tolerance in nonhalophytes. *Ann. Rev. Plant Physiol.* **31**:149–190.
- Grieve, C. M. and Suarez, D. L. 1997. *Purslane* (Portulaca oleracea L.): a halophytic crop for drainage water reuse systems. *PLSOA* **192**:277–283.
- Guy, R. and Reid, D. 1986. Photosynthesis and the influence of CO₂-enrichment on delta ¹³C values in a C₃ halophyte. *Plant Cell Environ.* **9**:65–72.
- Guy, R., Reid, D., and Krause, H. 1980. Shifts in carbon isotope ratios of two C₃ halophytes under natural and artificial conditions. *Oecologia* **44**:241–247.
- Hassidim, M., Braun, Y., Lerner, H., and Reinhold, L. 1990. Na⁺/H⁺ and K⁺/H⁺ antiport in root membrane vesicles isolated from the halophyte *Atriplex* and the glycophyte cotton. *Plant Physiol.* **94**:1795–1801.
- Hedrich, R. and Neher, E. 1987. Cytoplasmic calcium regulates voltage dependent ion channels in plant vacuoles. *Nature* **329**:833–836.
- Hothem, R. and Ohlendorf, H. 1989. Contaminants in foods of aquatic birds at Kesterton Reservoir, California, 1985. *Arch. Environ. Contam. Toxicol.* **18**:773–786.
- Jacoby, B. and Rudich, B. 1980. Proton-chloride symport in barley roots. *Ann. Bot.* **46**:493–498.
- Jeschke, W. D., Klagges, S., Hilpert, A., Vhatti, A. S., and Sarwar, G. 1995. Partitioning and flows of ions and nutrients in salt-treated plants of

- Leptochloa fusca* L. Kunth. *New Phytol.* **130**:23–35.
- Karajeh, F., Tanji, K., and King, I. 1994. Agroforestry drainage management model. I. Theory and validation. *J. Irri. Drain. Eng.* **120**:363–381.
- Karaheh, F. and Tanji, K. 1994a. Agroforestry drainage management model. II. Field water flow. *J. Irri. Drain. Eng.* **120**:382–396.
- Karajeh, F. and Tanji, K. 1994b. Agroforestry drainage management model. III. Field salt flow. *J. Irrig. Drain. Eng.* **120**:397–413.
- Kastner, K. and Sze, H. 1987. Potential-dependent anion transport in tonoplast vesicles from oat roots. *Plant Physiol.* **83**:483–489.
- Katsuhara, M., Yazaki, Y., Sakano, K., and Kawasaki, T. 1997. Intracellular pH and proton-transport in barley root cells under salt stress: in vivo ³¹P-NMR study. *Plant Cell Physiol.* **38**:155–160.
- Keiffer, C. and Ungar, I. 1997a. The effect of extended exposure to hypersaline conditions on the germination of five inland halophyte species. *Am. J. Bot.* **84**:104–111.
- Keiffer, C. and Ungar, I. 1997b. The effects of density and salinity on shoot biomass and ion accumulation in five inland halophytic species. *Can. J. Bot.* **75**:96–107.
- Kirsch, M., Zhigang, A., Viereck, R., Low, R., and Rausch, T. 1996. Salt stress induces an increased expression of V-type H⁺-ATPase in mature sugar beet leaves. *Plant Mol. Biol.* **32**:543–547.
- Koheil, M. A. H., Hilal, S. H., El-Alfy, T. S., and Leistner, E. 1992. Quaternary ammonium compounds in intact plants and cell suspension cultures of *Atriplex semibaccata* and *A. halimus* during osmotic stress. *Phytochemistry.* **31**:2003–2008.
- Koehl, K. 1997. The effect of NaCl on growth, dry matter allocation and ion uptake in salt marsh and inland populations of *Armeria maritima*. *New Phytol.* **135**:213–225.
- Koehl, K. 1997. NaCl homeostasis as a factor for the survival of the evergreen halophyte *Armeria maritima* (Mill.) Willd. under salt stress in winter. *Plant Cell Environ.* **20**:1253–1263.
- Kramer, D. 1984. Cytological aspects of salt tolerance in higher plants. In: *Salinity Tolerance in Plants: Strategies for Crop Improvement*. pp. 3–15.
- Staples, R. and Toenniessen, G., Eds., John Wiley, New York.
- Kremer, P. and Van Andel, J. 1995. Evolutionary aspects of life forms in angiosperm families. *Acta Bot. Neerl.* **44**:469–479.
- Kurkova, E. B. and Balnokin, Yu V. 1994. Pinocytosis and its possible role in ion transport in halophyte salt-accumulating organ cells. *Fiziol. Biokhim. Kul't. Rast. (Moscow)* **41**:578–582.
- Kurkova, E. B., Balnokin, Yu V., and Myasoedov, N. A. 1992. Some ultrastructural peculiarities and accumulation of sodium and chloride ions in cells of a halophyte *Petrosimonia triandra*. *Fiziologiya Biokhim. Kul't. Rast. (Moscow)* **39**:32–39.
- Leach, R., Wheeler, K., Flowers, T., and Yeo, A. 1990. Molecular markers for ion compartmentation in cells of higher plants. *J. Exp. Bot.* **41**:1089–1094.
- Le Houerou, H. N. 1993. Salt-tolerant plants for the arid regions of the Mediterranean isoclimatic zone. In: *Towards the Rational Use of High Salinity Tolerant Plants*, Vol. 1. pp. 403–422. Lieth, H. and Masoom, A., Eds., Kluwer Academic Publishers, Dordrecht.
- Le Houérou, H. N. 1996. Forage halophytes in the Mediterranean basin. In: *Halophytes and Biosaline Agriculture*. pp. 115–136. Chakour-Allah, R., Malcolm, C. V., and Hamdy, A., Eds., Marcel Dekker, New York.
- Li, X. G. and Gallagher, J. L. 1996. Expression of foreign genes, GUS and hygromycin resistance, in the halophyte *Kosteletzkya virginica* in response to bombardment with particle inflow gun. *J. Exp. Bot.* **47**:1437–1447.
- Lin, H., Salus, S., and Schumaker, K. 1997. Salt sensitivity and the activities of the H⁺-ATPases in cotton seedlings. *Crop Sci.* **37**:190–197.
- Lipshitz, N. and Waisel, Y. 1982. Adaptation of plants to saline environments: salt excretion and glandular structure. In *Tasks for Vegetation Science*, pp. 197–214. Sen, D. and Rajpurohit, K., Eds., Dr. W. Junk, The Hague.
- Llerena-V, F. A. 1994. Massive propagation of halophytes (*Distichlis spicata* and *Tamarix spp.*) on highly saline alkaline soils in the ex-Lake Texcoco, Mexico. In: *Halophytes as a Resource for Livestock and for Rehabilitation of Degraded Land*. pp. 289–292. Squires, V. R. and Ayoub, A., Eds., Kluwer Academic, Netherlands.

- Low, R., Rockel, B., Kirsch, M., Ratajczak, R., Hortensteiner, S., Martinoia, E., Luttge, U., and Rausch, T. 1996. Early salt stress effects on the differential expression of vacuolar H⁺-ATPase genes in roots and leaves of *Mesembryanthemum crystallinum*. *Plant Physiol.* **110**:259–265.
- Maathuis, F. J. M., Flowers, T. J., and Yeo, A. R. 1992. Sodium chloride compartmentation in leaf vacuoles of the halophyte *Suaeda maritima* (L.) Dum. and its relation to tonoplast permeability. *J. Exp. Bot.* **43**:1219–1223.
- Malcolm, C. 1996. Economic and environmental aspects of the sustainable use of halophytic forages. **In:** *Halophytes and Biosaline Agriculture*. pp. 363–376. Choukr-Allah, R., Malcolm, C., and Hamdy, A., Eds., Marcel Dekner, New York.
- Marcum, K. B. and Murdoch, C. L. 1992. Salt tolerance of the coastal salt marsh grass *Sporobolus virginicus* L. Kunth. *New Phytol.* **120**:281–288.
- Martinoia, E., Schramm, M. Flugge, U., and Kaiser, G. 1987. Intracellular distribution of organic acids and inorganic anions in mesophyll cells: transport mechanisms in the tonoplast. **In:** *Plant Vacuoles*. pp. 407–416. Marin, B., Ed., NATO ASI Series, Plenum Press, New York.
- Matile, P. 1988. Biochemistry and function of vacuoles. *Annu. Rev. Plant Physiol.* **29**:193–213.
- Matoh, T., Ishikawa, T., and Takahashi, E. 1989. Collapse of ATP-induced pH gradient by sodium ions in microsomal membrane vesicles prepared from *Atriplex gmelini* leaves. Possibility of Na⁺/H⁺ antiport. *Plant Physiol.* **29**:1133–1140.
- Matsui, M., Hose, J. E., Garrahan, P., and Jordan, G. A. 1992. Developmental defects in fish embryos from Salton Sea, California. *B. Environ. Contam. Toxicol.* **48**:914–920.
- Matsushita, N. and Matoh, T. 1992. Characterization of Na⁺ exclusion mechanisms of salt-tolerant reed plants in comparison with salt-sensitive rice plants. *Physiol. Plant.* **83**:170–176.
- McCree, K. 1986. Whole-plant carbon balance during osmotic adjustment to drought and salinity stress. *Aust. J. Plant Physiol.* **13**:43–44.
- McCree, K. and Richardson, S. 1987. Salt increases the water use efficiency in water stressed plants. *Crop Sci.* **27**:543–547.
- Mennen, H., Jacoby, B., and Marschner, H. 1990. Is sodium proton antiport ubiquitous in plant cells? *J. Plant Physiol.* **137**:180–183.
- Miyamoto, S. 1996. Salt tolerance, water use and potential irrigation scheduling of halophytes. **In:** *Halophytes and Biosaline Agriculture*. pp. 181–220. Choukr-Allah, R., Malcolm, C., and Hamdy, A., Eds., Marcel Dekker, New York.
- Miyamoto, S., Glenn, E. P., and Olsen, M. 1996. Growth, water use and salt uptake of four halophytes irrigated with highly saline water. *J. Arid Environ.* **32**:141–159.
- Mudie, P. 1974. The potential economic uses of halophytes. **In:** *Ecology of Halophytes*. pp. 565–597. Reimold, R. and Queen, W., Eds., Academic Press, New York.
- Munns, R. 1993. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant Cell Environ.* **16**:15–24.
- Naidoo, G. 1994. Growth, water and ion relationships in the coastal halophytes *Triglochin Bulbosa* and *T. Striata*. *Environ. Exp. Bot.* **34**:419–426.
- National Research Council (U.S.). Panel on Saline Agriculture in Developing Countries. 1990. *Saline Agriculture: Salt-Tolerant Plants for Developing Countries*. National Academy Press, Washington, D.C.
- Nerd, A. and Pasternak, D. 1992. Growth, ion accumulation, and nitrogen fractioning in *Atriplex barclayana* grown at various salinities. *J. Range Manage.* **45**:164–166.
- Neumann, P. 1997. Salinity resistance and plant growth revisited. *Plant Cell Environ.* **20**:1193–1198.
- Niu, X., Bressan, R., Hasegawa, P., and Pardo, J. 1995. Ion homeostasis in NaCl stress environments. *Plant Physiol.* **109**:735–742.
- Niu, X., Damsz, B., Kononowicz, A., Bressan, R., and Hasegawa, P. 1996. NaCl-induced alterations in both cell structure and tissue-specific plasma membrane H⁺-ATPase gene expression. *Plant Physiol.* **111**:679–686.
- Niu, X., Narasimhan, M., Salzman, R., Bressan, R., and Hasegawa, P. 1993a. NaCl regulation of plasma membrane H⁺-ATPase gene expression in a glycophyte and a halophyte. *Plant Physiol.* **103**:713–718.

- Niu, X., Zhu, J., Narasimhan, M., Bressan, R., and Hasegawa, P. 1993b. Plasma membrane H⁺-ATPase gene expression is regulated by NaCl in the cells of the halophyte *Atriplex nummularia* L. *Planta* **190**:433–438.
- O'Leary, J. W. 1988. Saline environments and halophytic crops. **In:** *Arid Lands Today and Tomorrow: Proceedings of an International Research and Development Conference*. pp. 773–790. Whitehead, E. E., Hutchinson, C. F., Timmerman, B. N., and Varady, R. G., Eds., Westview Press, Boulder, CO.
- O'Leary, J. 1994. The agricultural use of native plants on problem soils. *Monogr. Theor. Appl. Genet.* **21**:127–143.
- O'Leary, J. and Glenn, E. 1994. Global distribution and potential for halophytes. **In:** *Halophytes as a Resource for Livestock and for Rehabilitation of Degraded Land*. pp. 7–17. Squires, V. R. and Ayoub, A., Eds., Kluwer Academic, Netherlands.
- Odum, E. P. 1974. Halophytes, energetics and ecosystems. **In:** *Ecology of Halophytes*. pp. 599–602. Reimold, R. J. and Queen, W. H., Eds., Academic Press, New York.
- Ong, C. and Tanji, K. 1993. Evaporative concentration of trace elements in a multicell agricultural evaporation pond. *J. Agri. Food Chem.* **41**:1507–1510.
- Ong, C., Tanji, K., Dahlgren, R., Smith, G., and Quek, A. 1995. Water quality and trace element evapo-concentration in evaporation ponds for agricultural waste water disposal. *J. Agri. Food Chem.* **43**:1941–1947.
- Osmond, C. B., Bjorkman, O., and Anderson, D. J. 1980. *Physiological Processes in Plant Ecology: Toward a Synthesis with Atriplex*. Springer-Verlag, New York.
- Pantoja, O., Dainty, J., and Blumwald, E. 1992. Cytoplasmic chloride regulates cation channels in the vacuolar membrane of plant cells. *J. Membrane Biol.* **125**:219–229.
- Pantoja, O., Dainty, J., and Blumwald, E. 1990. Tonoplast ion channels from sugar beet cell suspensions. *Plant Physiol.* **94**:1788–1794.
- Pasternak, D. and Nerd, A. 1995. Research and utilization of halophytes in Israel. **In:** *Halophytes and Biosaline Agriculture*. pp. 325–348. Chakour-Alalah, R., Malcolm, C. V., and Hamdy, A., Eds., Marcel Dekker, New York.
- Pasternak, D. and Pietro, S. 1985. Biosalinity in action: bioproduction with saline water. *PLSOA* **89**:1–413.
- Perera, L. K. R. R., Mansfield, T. A., and Malloch, A. J. C. 1994. Stomatal responses to sodium ions in *Aster tripolium*: a new hypothesis to explain salinity regulation in above ground tissues. *Plant Cell Environ.* **17**:335–340.
- Perera, L. K. R. R., Robinson, M. F., and Mansfield, T. A. 1995. Responses of the stomata of *Aster tripolium* to calcium and sodium ions in relation to salinity tolerance. *J. Exp. Bot.* **46**:623–629.
- Perera, L., Silva, D., and Mansfield, T. 1997. Avoidance of sodium accumulation by the stomatal guard cells of the halophyte *Aster tripolium*. *J. Exp. Bot.* **48**:707–711.
- Plant, P. J., Gelli, A., and Blumwald, E. 1994. Vacuolar chloride regulation of an anion-selective tonoplast channel. *J. Membrane Biol.* **140**:1–12.
- Poljakoff-Mayber, A., Somers, G., Werker, E., and Gallagher, J. 1994. Seeds of *Kosteletzkya virginica* (Malvaceae): their structure, germination and salt tolerance. *Am. J. Bot.* **81**:54–59.
- Pope, A. and Leigh, R. 1987. Some characteristics of anion transport at the tonoplast of oat roots, determined from the effects of anions on pyrophosphatase-dependent proton transport. *PLANA* **172**:91–100.
- Popp, M., Polania, J., and Weiper, M. 1993. Physiological adaptations to different salinity levels in mangrove. **In:** *Towards the Rational Use of High Salinity Tolerant Plants*, Vol. 1. pp. 217–224. Lieth, H. and Masoom, A., Eds., Kluwer, Dordrecht.
- Presser, T. 1994. The Kesterton effect. *Environ. Manag.* **18**:437–454.
- Quirk, J. P. 1971. Chemistry of saline soils and their physical properties. **In:** *Salinity and Waster Use*. pp. 79–91. Talsma, T. and Philip, J. R., Eds., Macmillan, London.
- Qureshi, R. H., Aslam, M., and Rafiq, M. 1991. Expansion in the use of forage halophytes in Pakistan. **In:** *ACIAR Proc.* pp. 12–16. A. C. T., Canberra.
- Ratajczak, R., Richter, J., and Luetge, U. 1994. Adaptation of the tonoplast V-type H⁺-ATPase of *Mesembryanthemum crystallinum* to salt stress,

- C-3-CAM transition and plant age. *Plant Cell Environ.* **17**:1101–1112.
- Rausch, T., Kirsch, M., Low, R., Lehr, A., Viereck, R., and Zhigang, A. 1996. Salt stress responses of higher plants: the role of proton pumps and Na⁺/H⁺-antiporters. *J. Plant Physiol.* **148**:425–433.
- Rea, P. A., Yongcheol, K., Sarafian, V., Poole, R. J., Davies, J. M., and Sanders, D. 1992. Vacuolar H⁺-translocating pyrophosphatases: a new category of ion translocase. *TIBS* **17**:348–353.
- Reimann, C. 1992. Sodium exclusion by *Chenopodium* spp. *J. Exp. Bot.* **43**:503–510.
- Reimann, C. and Breckle, S. W. 1993. Sodium relations in Chenopodiaceae: a comparative approach. *Plant Cell Environ.* **16**:323–328.
- Reimann, C. and Breckle, S. W. 1995. Salt tolerance and ion relations of *Salsola Kali* L.: differences between *tragus* (L.)
- Nyman and ssp. *ruthenica* (Iljin) Soo. *New Phytol.* **130**:37–45
- Rhoades, J. 1993. Practices to control salinity in irrigated soils. **In: Towards the Rational Use of High Salinity Tolerant Plants**, Vol. 2. pp. 379–387. Lieth, H. and Masoom, A., Eds., Kluwer Academic Publishers, Dordrecht.
- Rhoades, J., Bingham, F., Letey, J., Hoffman, G., Dedrick, A., Pinter, P., Alves, W., Swain, R., Pacheco, P., Lemert, R., and Replogle, J. 1989. Use of saline drainage water for irrigation: imperial valley study. *Agric. Water Manag.* **16**:25–36.
- Rhodes, D. and Hanson, A. 1993. Quarterly ammonium and tertiary sulfonium compounds in higher plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **44**:357–384.
- Richards, R. A. 1992. Increasing salinity tolerance of grain crops: is it worthwhile? *PLSOA* **146**:89–98.
- Riley, J., Fitzsimmons, K., and Glenn, E. 1998. Halophyte irrigation: an overlooked strategy for management of membrane filtration concentrate. *Desalination* **110**:197–211.
- Rozema, J. and Van Diggelen, J. 1991. A comparative study of growth and photosynthesis of four halophytes in response to salinity. *Acta Oecol.* **12**:673–682.
- Rozema, J., Zaheer, S., Niazi, B., Linders, H. and Broekman, R. 1993. Salt tolerance of *Beta vulgaris* L.: a comparison of the growth of sea-beet and fodder-beet in response to salinity. **In: Towards the Rational Use of High Salinity Tolerant Plants**, Vol. 2, pp. 193–198. Lieth, H. and Masoom, A., Eds., Kluwer Academic Publishers, Dordrecht.
- Rubio, F., Gassman, W., and Schroeder, J. 1995. Sodium-driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. *Science* **270**:1660–1663.
- Sanders, D. 1980. The mechanism of Cl⁻ transport at the plasma membrane of *Chara corallina*. I. Co-transport with H⁺. *J. Membr. Biol.* **53**:129–141.
- Schachtman, D., Lagudah, E., and Munns, R. 1992. The expression of salt tolerance from *Triticum tauschii* in hexaploid wheat. *Theoret. Appl. Genet.* **84**:714–719.
- Schachtman, D. and Schroeder, J. 1994. Structure and transport mechanisms of a high-affinity potassium uptake transporter from higher plants. *Nature* **370**:655–658.
- Schachtman, D., Tyerman, T., and Terry, B. 1991. The K⁺/Na⁺ selectivity of a cation channel in the plasma membrane of root cells does not differ in salt-tolerant and salt-sensitive wheat species. *Plant Physiol.* **97**:598–605.
- Schirmer, U. and Breckle, S. 1982. The role of bladders for salt removal in some Chenopodiaceae (mainly *Atriplex*) species. **In: Tasks for Vegetation Science**. pp. 215–232. Sen, D. and Rajpurohit, K., Eds., Dr. W. Junk, The Hague.
- Serrano, R. 1996. Salt tolerance in plants and microorganisms: toxicity targets and defense responses. *Int. Rev. Cyt.* **165**:1–52.
- Serrano, R. and Gaxiola, R. 1994. Microbial models and salt stress tolerance in plants. *Crit. Rev. Plant Sci.* **13**:121–138.
- Shalhevet, J. 1993. Plants under water and salt stress. **In: Plant Adaptation to Environmental Stress**. pp. 133–154. Fowden, L., Mansfield, T., and Stoddart, J., Eds., Chapman and Hall, New York.
- Somers, G. 1975. *Seed-Bearing Halophytes as Food Plants*. University of Delaware Sea Grant Program, College of Marine Studies, Newark, Delaware.
- Squires, V. R. and Ayoub, A. T. 1994. *Halophytes as a Resource for Livestock and for Rehabilitation of Degraded Lands*. Kluwer, Dordrecht.
- Staal, M., Maathuis, F., Elzenga, T., Overbeek, J., and Prins, H. 1991. Na⁺/H⁺ antiport activity of the salt-tolerant *Plantago maritima* and the salt-sensitive *Plantago media*. *Physiol. Plant.* **82**:179–184.

- Storey, R., Ahmad, N., and Wyn Jones, R. 1977. Taxonomic and ecological aspects of the distribution of glycinebetaine and related compounds in plants. *Oecologia* **27**:319–332.
- Swingle, R., Glenn, E., and Squires, V. 1996. Growth performance of lambs fed mixed diets containing halophyte ingredients. *Anim. Feed Sci. Technol.* **63**:137–148.
- Thiyagarajah, M., Fry, S., and Yeo, A. 1996. *In vitro* salt tolerance of cell wall enzymes from halophytes and glycophytes. *J. Exp. Bot.* **47**:1717–1724.
- Thomas, J. C. and Bohnert, H. J. 1993. Salt stress perception and plant growth regulators in the halophyte *Mesembryanthemum crystallinum*. *Plant Physiol.* **103**:1299–1304.
- Troyo-Dieguez, E., Ortega-Rubio, A., Maya, Y., and Leon, J. L. 1994. The effect of environmental conditions on the growth and development of the oil-seed halophyte *Salicornia bigelovii* Torr. in arid Baja California Sur, Mexico. *J. Arid Environ.* **28**:207–213.
- Tyerman, S. 1992. Anion channels in plants. *Annu. Rev. Plant Physiol. Mol. Biol.* **43**:351–373.
- Ungar, I. 1991. *Ecophysiology of Vascular Halophytes*. CRC Press, Boca Raton.
- Ungar, I. 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). *Am. J. Bot.* **83**:604–607.
- van Schilfhaarde, J. 1993. Water management strategies for salinity control. **In: Towards the Rational Use of High Salinity Tolerant Plants**, Vol. 2. pp. 371–378. Lieth, H. and Masoom, A., Eds., Kluwer Academic Publishers, Dordrecht.
- Warwick, N. and Halloran, G. 1992. Accumulation and excretion of sodium, potassium and chloride from leaves of two accessions of *Diplachne fusca* (L.) Beauv. *New Phytol.* **121**:53–61.
- Watson, M. C., Banuelos, G. S., O'Leary, J. W., and Riley, J. J. 1994. Trace element composition of *Atriplex* grown with saline drainage water. *Agric. Ecosyst. Environ.* **48**:157–162.
- Watson, M. C., 1990. *Atriplex* species as irrigated forage crops. *Agric. Ecosystems Environ.* **32**:107–118.
- Watson, M. and O'Leary, J. W. 1993. Performance of *Atriplex* species in the San Joaquin Valley, California, under irrigation and with mechanical harvests. *Agric. Ecosystems Environ.* **43**:255–266.
- Weiglin, C. and Winter, E. 1991. Leaf structures of xerohalophytes from an East Jordanian Salt Pan. *Flora (Jena)* **185**:405–424.
- Wescott, D. 1988. Reuse and disposal of higher salinity subsurface drainage water — a review. *Agric. Water Manag.* **14**:483–511.
- Wilson, C., Clark, R. A., and Shearer, G. C. 1994. Effect of salinity on the plasma-membrane ATPase from tomato (*Lycopersicon-Esculentum* Mill) leaves. *Plant Sci.* **103**:1–9.
- Wyn Jones, R. G. and Gorham, J. 1986. The potential for enhancing the salt tolerance of wheat and other important crop plants. *Outlook Agric.* **15**:33–39.
- Yensen, N. P., Yensen, S. B., and Weber, C. W. 1988. A review of *Distichlis* spp. For production and nutritional values. **In: Arid Lands Today and Tomorrow: Proceedings of an International Research and Development Conference**. pp. 809–822. Whitehead, E. E., Hutchinson, C. F., Timmerman, B. N., and Varady, R. G., Eds., Westview Press, Boulder, CO.
- Yeo, A. 1994. Physiological criteria in screening and breeding. **In: Soil Mineral Stresses, Approaches to Crop Improvement**. pp. 11– 36. Yeo, A. and Flowers, T., Eds., Springer-Verlag, Berlin.
- Yeo, A. and Flowers, T. 1986. Ion transport in *Suaeda maritima*: its relation to growth and implications for the pathway of radial transport of ions across the root. *J. Exp. Bot.* **37**:143–159.
- Zhu, J. K., Hasegawa, P. M., and Bressan, R. A. 1997. Molecular aspects of osmotic stress in plants. *Clin. Rev. Plant Sci.* **16**:253–277.
- Zimmermann, U., Rygol, J., Balling, A., Klock, G., Metzler, A., and Haase, A. 1992. Radial turgor and osmotic pressure profiles in intact and excised roots of *Aster tripolium*. Pressure probe measurements and nuclear magnetic resonance-imaging analysis. *Plant Physiol.* **99**:186–196.
- Zurayk, R. and Baalbaki, R. 1996. *Inula crithmoides*: a candidate plant for saline agriculture. *Arid Soil Res. Rehabil.* **10**:213–223.

