CHAPTER 11

SALINE TOLERANCE PHYSIOLOGY IN GRASSES

KENNETH B. MARCUM

Department of Applied Biological Sciences
Arizona State University

1. INTRODUCTION

Salinization of agricultural lands is accelerating, with over 1 Mha of irrigated lands deteriorating to non-productivity each year (Hamdy, 1996; Choukr-Allah, 1996). Currently from 100 Mha to 1000 Mha of irrigated land is salt-affected due to human activity (Szabolcs, 1989; Oldeman et al., 1991). Though much of this land is currently too saline for conventional agriculture, it has the potential for growing salt tolerant forages, grasses (Poaceae) playing a dominant role (Ghassemi & Jakeman, 1995).

With over 7,500 species, the Poaceae inhabit the earth in greater numbers, and have a greater range of Chlorideimatic adaptation than any other plant family (Hitchcock, 1971; Gould & Shaw, 1983). Therefore, it is not surprising that grasses show an extreme range in salinity tolerance, from salt-sensitive (ex. meadow foxtail *Alopecurus pratensis* L.), to salt-tolerant halophytic (ex. saltgrass *Distichlis spicata* L.) (Richards, 1954; Maas, 1986; Aronson, 1989).

In this paper growth responses and physiological adaptations to salinity of eight C_4 grass species studied in my lab will be discussed, representing an extreme range of tolerance. Physiological mechanisms of salt tolerance will be discussed, and cross-referenced to salinity studies involving other grass species. The grasses, listed in (Table 1), will be indicated in this paper by genus, except for *Sporobolus*, where genus abbreviation is followed by species names.

1.1. Growth responses to salinity and relative salinity tolerance

1.1.1. Shoot Growth Responses

Plant salinity tolerance depends not only on genotype, but also on environmental and

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cultural conditions. Therefore, absolute salinity tolerance cannot be determined with certainty, but rather on a relative basis (to other genotypes), given uniform growing conditions (Maas & Hoffman, 1977; Maas, 1986). Growth indicators used in these studies (shoot weight, % canopy leaf firing, rooting depth, and root weight) were highly correlated with one another (r^2 ranging from 0.65 to 0.8), indicating their mutual effectiveness in predicting relative salinity tolerance.

Table 1. *Grasses studied.*

Scientific Name	*Common Name*
Bouteloua curtipendula (Michx.) Torr.	Sideoats grama
Buchlon dactyloides (Nutt.) Engelm.	Buffalograss
Cynodon dactylon (L.) Pers.	Bermudagrass
Distichlis spicata var. *stricta* (Torr.) Beetle	Desert saltgrass
Sporobolus airoides (Torr.) Torr.	Alkali sacaton
Sporobolus cryptandrus (Torr.) Torr.	Sand dropseed
Sporobolus virginicus (L.) kunth	Seashore dropseed
Zoysia japonica Steud.	Japanese lawngrass

Relative salinity tolerance is often quantified as the salt level resulting in a 50% reduction in shoot growth (yield), or alternatively, the threshold salinity, i.e. salinity level where yield begins to decline, followed by the rate, or slope, of yield reduction (Maas & Hoffman, 1977; Carrow & Duncan, 1998). Fifty percent shoot growth reduction occurred at media salinities ranging from 140 mM (approximately 11 dS m^{-1}) for *Bouteloua*, to >600 mM (>46 dS m^{-1}) for *Distichlis* (Figure 1). Using this as criteria, salinity tolerance decreased in the order: *Distichlis* = S. vi*rginicus* > *S. airoides* > *Cynodon* > *Zoysia* > *S. cryptandrus* > *Bouteloua* = *Buchlon*. Reid et al. (1993) also reported 50% shoot growth decline at 12 dS m^{-1} for three *Buchlon* cultivars. Data for *Zoysia* reveals a high genetic diversity, with 50% shoot growth reduction occurring from 170 to 375 mM Na Chloride, depending on cultivar or accession (Marcum & Murdoch, 1994; Marcum et al., 1998). Genetic diversity is also seen within the *Cynodon* genus (de Wet & Harlan, 1970). Fifty percent shoot growth reductions for bermudagrass cultivars and/or accessions has been reported as 24 and 33 dS m^{-1} (Dudeck & Peacock, 1993),2 4 and 31 dS m^{-1} (Francois, 1988), and 17 to 22 dS m^{-1} (Dudeck et al., 1983). The halophytic nature of *S. airoides*, *S. virginicus*, and *Distichlis* has been reported (Butler et al., 1974; Maas & Hoffman, 1977; Aronson, 1989; Marcum & Murdoch, 1992). In several studies, shoot growth of *Distichlis* was not affected by salinities up to 40 dS m^{-1} (Parrondo, 1978; Kemp et al., 1981).

Salt-sensitive plants (glycophytes) and moderately salt-tolerant plants (mesophytes) generally have a flat yield response to salinity prior to a threshold salinity level, beyond which shoot growth declines. In contrast, highly salt-tolerant plants often display stimulated shoot, and root growth at moderate salinity levels, followed by yield de cline (Maas & Hoffman, 1977; Maas, 1986; Carrow et al., 1998). Increased shoot growth (relative to control) under moderate salinity (100 mM

Na Chloride, or 8 dSm^{-1}) was evident in *Distichlis*, *S. airoides* and *S. virginicus* (Figure 1). All other grasses displayed progressive shoot growth reductions at all salinity levels. Salt-stimulated shoot growth has been observed in other salt tolerant and halophytic grasses. Shoot growth peaked at 90 mM Na Chloride (8 dSm^{-1}), then declined in *Halopyrum mucronatum* (L.) Stapf, a perennial grass found on coastal dunes of Pakistan (Khan et al., 1999). Shoot growth was stimulated with increasing salinity up to 25 mM Na Chloride (2.5 dSm^{-1}), then declined, in 2 of 6 *Sporobolus* species studied (*S. stapfianus* and *S. pellucidus*) (Wood & Gaff, 1989).

1.1.2. Root Growth Responses

Root growth stimulation (increased root mass, rooting depth, or both) in salt tolerant grasses is typically a more common, accentuated response to moderate salinity stress than shoot growth stimulation (Maas & Hoffman, 1977). The net result is generally an increase in root/shoot ratios, which may be a salinity tolerance mechanism to counter low external water potential by increasing plant absorptive area (Bernstein & Hayward, 1958; Donovan & Gallagher, 1985). Increased rooting depth, relative to control plants, was observed in *Distichlis*, *S. airoides*, *S. virginicus,* and *Cynodon* under salinity stress (Figure 1). However, relative rooting depth de Chlorideined at high salinity for *Cynodon*, but not in the halophytic grasses. In contrast, rooting depth of *Buchlon*, *Bouteloua*, and *S. cryptandrus* progressively declined with increasing salinity stress.

Root stimulation has been observed in a number of salt tolerant and halophytic grasses. Root dry weights linearly increased with increasing salinity up to 450 mM Na Chloride (35 dS m^{-1}) in *S. virginicus*, resulting in a root/shoot ratio of 2.2, relative to 0.5 (control) (Marcum, 1992). Blits and Gallagher (1991) reported a doubling in root mass of *S. virginicus* grown in seawater, relative to fresh water. Though root growth (length) increased under moderate salinity stress, relative to control, shoot growth de clined in *Chloris gayana* L. (Waisel, 1985), *Cynodon* (Ackerson & Youngner, 1975), and *Zoysia* (*Zoysia japonica* Steud. and *Z. matrella* [L.] Merr.) (Marcum & Murdoch, 1990). Rooting decline under even mild salinity stress has been previously reported in *Buchlon* (Wu & Lin, 1993), and in other moderate to salt-sensitive grasses, such as *Poa pratensis* L. (Torello & Symington, 1984), *Paspalum notatum* Flugge (Dudeck & Peacock, 1993), and *Festuca rubra* L. (Khan & Marshall, 1981). Total root dry weight (data not shown) was highly correlated with rooting depth (r=0.83).

1.2. Physiological adaptations to salinity

1.2.1. Ion Exclusion

It has long been accepted that the major causes of plant growth inhibition under salinity stress are osmotic stress (osmotic inhibition of plant water absorption), and specific ion effects, including toxicities and imbalances (Bernstein & Hayward, 1958; Greenway et al., 1966; O'Leary, 1971). In comparison to salt tolerant, or halophytic dicotyledonous

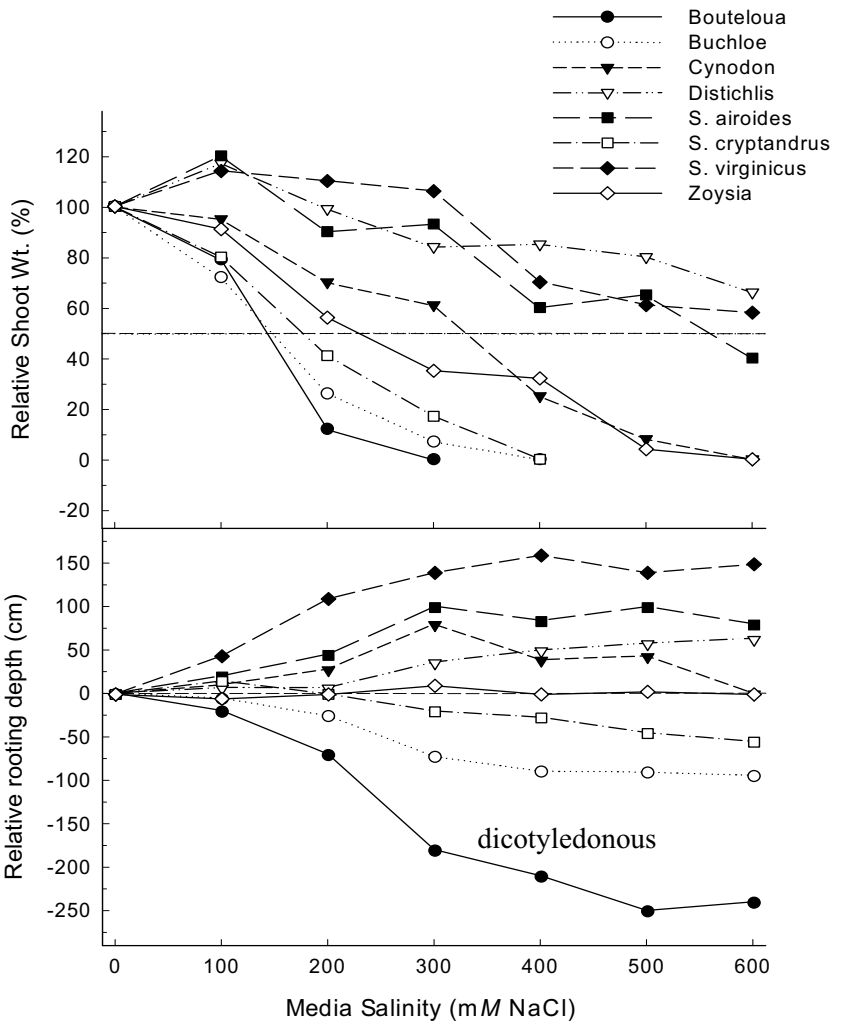

Figure 1. *Relative shoot dry weight [(treatment wt./control wt.) X 100] and relative rooting depth (salinity treatment length minus control length) of grasses exposed to increasing salinity levels in solution culture. Vertical bars represent LSD ($P < 0.05$) values for mean comparison at each salinity level.*

plants, monocots (including Poaceae) tend to exclusion saline ions from shoots, thereby minimizing toxic effects (Albert & Popp, 1977; Gorham et al., 1985, 1993). Saline ion exclusion from shoots was strongly associated with salinity tolerance among these eight grasses representing the range of salinity tolerance present in the Poaceae (Figure 2). Sodium shoot ion content mirrored that of Chloride, and is not shown. Chloride and Na^+ accumulated to extremely high levels in *Bouteloua* shoots,

and high levels in *Buchlon* and *S. cryptandrus* shoots, but was maintained at concentrations similar to the growth media in *Cynodon* and halophytic *Distichlis*, *S. virginicus*, and *S. airoides* shoots, particularly at high salinity. Salinity tolerance of other grasses has been related to saline ion exclusion. Salinity tolerance in *Sorghum halepense* (L.) Pers., relative to *Sorghum bicolor* (L.) Moench was associated with shoot Cl^- concentration (Yang et al., 1990). Similarly, salt-tolerant *Agropyron elongatum* (Host) Palisot de Beauvois accessions ex Chlorideuded Na^+ and Cl^- from shoots (while maintaining fairly high K^+ contents) to a greater extent than salt-sensitive *Agropyron desertorum* (Fisch. ex Link) Schult. accessions (Johnson, 1991). In contrast, salt-tolerant *Puccinellia distans* (L.) Parl and *P. lemmoni* (Vasey) Scribn. were found to accumulate more Na^+ and Cl^- in shoots than did moderately salt-tolerant *Agrostis stolonifera* L. (Harivandi & Butler, 1992).

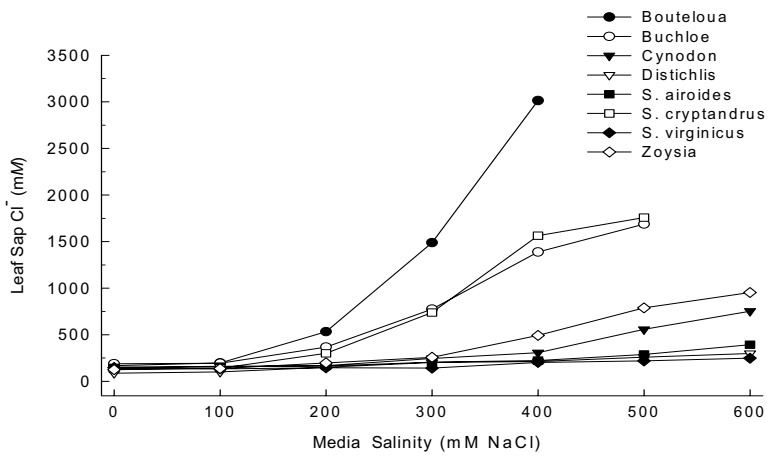

Figure 2. *Leaf sap Chloride$^-$ levels of grasses exposed to increasing salinity levels in solution culture.*

Saline ion exclusion also appears to be an important factor influencing intraspecies salinity tolerance, i.e. at the cultivar or accession level. For example, salt-sensitive populations were found having, at a given test salinity, higher shoot Na^+ and Chloride than coastal (or other saline-site) salt-tolerant accessions in *Festuca rubra* L. (Hannon & Barber, 1972; Khan & Marshall, 1981), *Cynodon* (Ramakrishnan & Nagpal, 1972), and *Agrostis stolonifera* L. (Wu, 1981). Relative salinity tolerance of *Zoysia* cultivars and accessions have successfully been predicted on the basis of shoot Na^+ concentrations occurring under salt stress (Marcum et al., 1998; Marcum, 2003).

1.2.2. Osmotic Adjustment and Ion Regulation

Osmotic stress due to lack of osmotic adjustment, resulting in reduced water absorption and physiological drought, has long been considered a major cause of salinity injury in plants (Bernstein & Hayward, 1958; Levitt, 1980; Harivandi et al., 1992). Maintenance of cell turgor and plant growth requires sufficient increase in sap

osmolality to compensate for external osmotic stress, the process of osmoregulation, or osmotic adjustment (Hellebust, 1976; Levitt, 1980). In a saline environment, osmotic adjustment is needed to avoid osmotic stress, yet this may result in ion toxicity (Yeo, 1983; Gorham et al., 1985).

It has been noted that monocots (relative to salt-tolerant dicots), including Poaceae, tend to restrict saline ion uptake. This has been suggested to cause cell dehydration and reduced growth under saline conditions, due to lack of osmotic adjustment (Albert & Popp, 1977; Gorham et al., 1980; Gorham, 1985). Indeed, declining shoot water content is commonly observed in grasses under salinity stress (Greenway et al., 1966; Greenway & Munns, 1980; Weimberg & Shannon, 1988; Marcum & Murdoch, 1990), though slight increase in shoot succulence under moderate salinity has been noted in some grass halophytes (Blits & Gallagher, 1991; Marcum & Murdoch, 1992; Khan et al., 1999). However, complete osmotic adjustment occurred in all eight grasses, sap osmolalities being maintained below (more negative than) media osmolality (Figure 3). In fact, salt-sensitive grasses osmotically adjusted to a much greater degree than salt-tolerant ones. Among the eight grasses, shoot sap osmolality was highly negatively correlated with salinity tolerance and root growth under salt stress ($r>-0.8$). Complete osmotic adjustment under salinity stress has been reported previously in a range of grasses (Peacock & Dudeck, 1985; Wyn Jones & Gorham, 1989; Marcum & Murdoch, 1990). In these studies, shoot sap osmolality level was negatively correlated with salinity tolerance. In other words, in salt tolerant grasses, osmotic adjustment, though complete, is nevertheless minimized, i.e. shoot sap osmolality is maintained Chlorideose to saline media levels.

Though salinity tolerance in grasses is clearly associated with saline ion exclusion, Na^+ and $Chloride^-$ have been instrumental for shoot osmotic adjustment in a number of studies, comprising the majority of osmotically active solutes (Marcum & Murdoch, 1990; Warwick & Halloran, 1991; Marcum & Murdoch, 1992; Khan et. al., 1999). Among these eight grasses, shoot Na^+ and Cl^- concentrations were highly correlated with osmotic adjustment ($r=0.9$). Therefore, though saline ion exclusion is clearly critical for salinity tolerance in grasses, saline ion regulation, rather than exclusion, may be a more apt description of the salinity tolerance mechanism operating in grasses.

Saline ion regulation in grasses may occur in several ways. Selectivity for K^+ over Na^+ may occur by selective K^+ absorption-vacuolar Na^+ compartmentation in root cortical cells or endodermis, or by selective saline ion excretion through specialized salt glands or bladders (Levitt, 1980; Kramer, 1984; Jeschke, 1984; Daines & Gould, 1985; Garbarino & Dupont, 1988). In glycophytic grasses, tissue Na^+ may be reabsorbed from the xylem via mature xylem parenchyma cells in roots or shoots, and translocated back to soil (Yeo et al., 1977; Jeschke, 1979; Taleisnik, 1989). Alternately, ion partitioning may occur, whereby saline ions are redistributed to mature, senescing leaves or other organs (Lessani & Marschner, 1978; Yeo & Flowers, 1984; Bhatti et al., 1993; Jeschke et al., 1995).

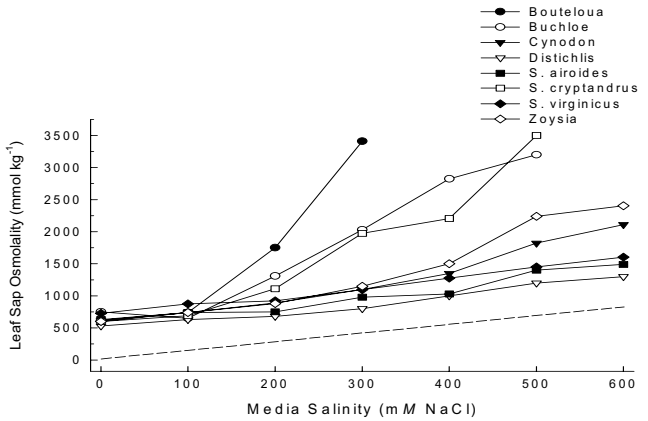

Figure 3. *Leaf sap osmolality of grasses exposed to increasing salinity levels in solution culture.*

1.2.3. Glandular Ion Excretion

Salt glands or bladders are present in a number of salt-adapted species, which eliminate excess saline ions from shoots by excretion (Waisel, 1972; Liphschitz & Waisel, 1982; Fahn, 1988). Multicellular epidermal salt glands are present in several families of dicotyledons, e.g. Frankeniaceae, Plumbaginaceae, Aviceniaceae, and Tamaricaceae (Waisel, 1972; Fahn, 1988). Within the Poaceae, bicellular epidermal salt glands have been reported to occur in over 30 species within the tribes Chlorideae, Eragrosteae, Aeluropodeae, and Pappophoreae (Liphshchitz & Waisel, 1974; Taleisnik & Anton, 1988; Amarasinghe & Watson, 1989), members of the subfamily Chloridoideae (Gould & Shaw, 1983; Chlorideayton & Renvoize, 1986).

Salt glands of the Poaceae are, in outward appearance, similar to leaf epidermal bicellular microhairs. Though microhairs resembling salt glands have been observed in all grass subfamilies except Pooideae (Liphschitz & Waisel, 1982; Amarasinghe & Watson, 1988), functioning salt glands have been found only within the subfamily Chloridoideae (Amarasinghe & Watson, 1988; Amarasinghe & Watson, 1989). This is probably due to an ultrastructural modification hypothesized to be responsible for salt excretion in Chloridoid grasses: a series of parallel, invaginated plasma membrane channels within the gland's basal cell (Liphschitz & Waisel, 1982; Oross & Thomson, 1982a; Oross & Thomson, 1982b). These membranes are actually infoldings of the plasmalemma that originate adjacent to the wall separating the cap and basal cells, forming open channels in the direction of ion flow. Ultracytochemical localization of ATPase activity within salt gland basal cells of *S. virginicus* supports the hypothesis of active ion loading at these sites (Naidoo & Naidoo, 1999). In addition, there are numerous mitochondria associated with the parallel membranes, probably involved in providing an energy supply for channel ion loading (Levering & Thomson, 1971; Naidoo & Naidoo, 1999).

Salt glands in the Poaceae, structurally distinct from the multicellular glands of dicots, consist of a basal cell, attached, or imbedded, into the leaf epidermis, and a

cap cell (73, 74) (Figure 5A). The glands are characterized by cutinized cell walls, and are often surrounded by papillae. Though the basic, bicellular structure is the same in all Chloridoid species, their appearance varies (Liphschitz & Waisel, 1982) (Figure 5). In some species, glands are sunken into the epidermis, with the basal cell totally imbedded, ex. *Distichlis* (Figure 5H). In others, the basal cell is semi-imbedded, ex. *Cynodon* (Figure 5G). Finally, the basal cell may extend out from the epidermis, with the gland lying recumbent to the leaf surface, ex. *Bouteloua* (Figure 5B). Salt glands of Poaceae are quite small (usually 25-70 μm in length), though size may vary substantially, from imbedded to elongated, protruding types. Glands range in size from 15 μm in length in *Distichlis* (Marcum, 1990), 35 μm in Zoysia (Marcum & Murdoch, 1996), to 70 μm in *Buchlon* (Marcum, 1999) (Figure 5). Salt glands have been found on both abaxial and adaxial leaf surfaces of excreting species (Marcum & Murdoch, 1996; Liphshchitz & Waisel, 1974; Marcum, 1999). Glands are longitudinally arranged in parallel rows atop intercostal regions of leaves, adjacent to rows of stomates (Figure 5A).

Evidence that salt gland ion excretion is an active, metabolically driven process is varied, including effects of temperature (Pollak & Waisel, 1979), light (Pollak & Waisel, 1970), oxygen pressure (Liphschitz & Waisel, 1982), and metabolic inhibitors (84) on excretion rate, as well as selectivity of ion excretion. Excretion is typically highly selective for Na^+ and Cl^- (Wieneke et al., 1987; Arriaga, 1992; Worku & Chapman, 1998), though other ions may be excreted in minute amounts, such as K^+, Ca^{2+}, and Mg^{2+} (Liphschitz & Waisel, 1982; Marcum & Murdoch, 1990, 1994; Naidoo & Naidoo, 1998). Comparison of salt gland excretion rates among studies is difficult, due to the varying influence of environmental factors, such as light and temperature, cumulative days of exposure to salt stress, and plant factors, such as leaf age (Jeschke et al., 1995). Also, units of measurement differ, one fundamental difference being whether excretion rates are based on leaf area or leaf weight. Finally, excretion rate is not static, but is influenced by saline ion concentrations in the growing media. Increasing media salinity generally stimulates excretion up to an optimal level, above which excretion rate may decline (Liphschitz & Waisel, 1982). Maximum excretion rate was reported to occur at 150 to 200 mM media Na Chloride (8-13 dSm^{-1}) in moderately tolerant Chloridoid species such as *Cynodon*, *Rhodesgrass*, goosegrass [*Eleusine indica* (L.) Gaertn.], and Kallargrass (Wieneke, 1987; Liphshchitz & Waisel, 1994; Worku & Chapman, 1998). However, excretion was maximal at 200 mM Na Chloride (17 dSm^{-1}) in *Distichlis* and *Spartina* spp. (Liphschitz & Waisel, 1982), and 300 mM Na Chloride (23 dSm^{-1}) in *S. virginicus* (Marcum & Murdoch, 1992).

Among the C_4 grasses reported here, shoot Na^+ and $Chloride^-$ concentrations were negatively correlated, while salt tolerance was positively correlated with salt gland Na^+ and Cl^- excretion rates. (Table 2) shows ion excretion rates for the eight grasses. Note that *S. virginicus* had Na^+ and Cl^- excretion rates 35 and 38 times higher, respectively, than *Buchlon*. Similar strong correlations between salt gland excretion rates, shoot Na^+ and Cl^- concentrations, and salinity tolerance were observed among three C_4 grasses in another study (Marcum & Murdoch, 1994).

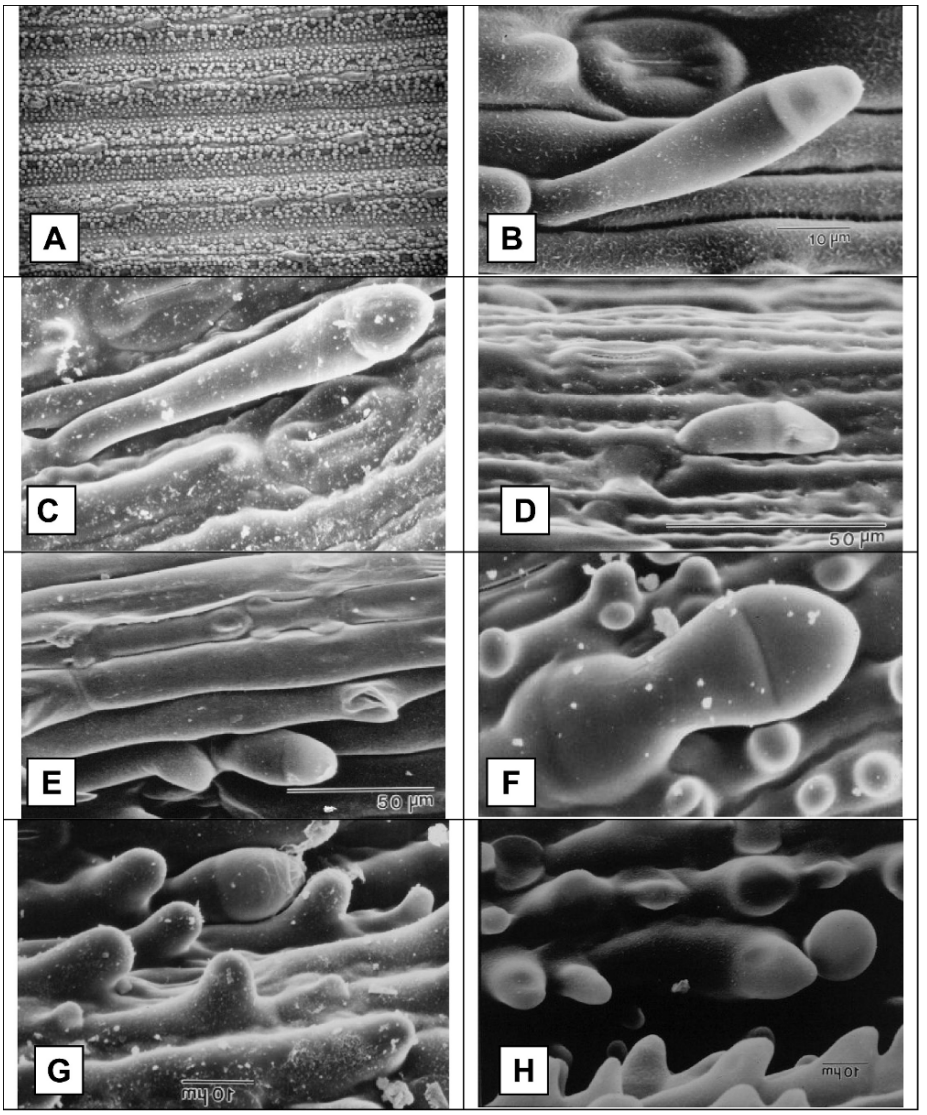

Figure 4. Scanning electron micrographs of adaxial leaf surfaces.A: Overview of Zoysia *(*Zoysia matrella *(L.) Merr.) leaf surface, showing location of salt gland relative to other structures.*
B: Salt gland of Bouteloua curtipendula. *C: Salt gland of* Buchlon dactyloides.
D: Salt gland of Sporobolus cryptandrus. *E: Salt gland of* Sporobolus airoides.
F: Salt gland of Zoysia japonica. *G: Salt gland of* Cynodon dactylon.
H: Salt gland of Distichlis spicata.
Key to photo labels: B = basal cell, C = cap cell, G = salt gland, I = Intercostal zone of leaf epidermis, P = papilla, S = stomate/stomata.

Sodium and Chloride$^-$ excretion rates were negatively correlated to shoot concentrations, but positively correlated to leaf salt gland density and salinity

tolerance among 57 *Zoysia* grasses species (Marcum & Murdoch, 1990; Marcum et al., 1998). Excretions rates of various *Zoysia* spp. reported range from 130 µmol Na^+/g leaf dry wt./week in salt-sensitive *Zoysia japonica* to 730 µmol Na^+/g leaf dry wt./week in salt-tolerant *Zoysia matrella*, with gland densities ranging from 28/mm^2 leaf surface in salt-sensitive *Zoysia japonica* to 100/mm^2 in salt-tolerant *Zoysia macrostachya* Franch. & Sav.

Table 2. *Leaf salt gland $Chloride^-$ and Na^+ excretion rates[a] of three* Chloridoid grasses. *Ion excretion measured in plants exposed to 200 mM Na Chloride.*

Grass	*$Chloride^-$*	*Na^+*
S. virginicus	2104	2540
Distichlis	1268	1130
S. airoides	563	565
Zoysia	423	130
Cynodon	394	87
S. cryptandrus	85	65
Bouteloua	56	65
Buchlon	42	51
$LSD_{0.05}$	56	72

[a]*Excretion rates in µmol ion/g leaf dry wt./week.*

1.2.4. Ion Compartmentation and Compatible Solutes

In vitro studies have shown that enzymes of both glycophytes and halophytes have similar sensitivities to salt, being inhibited at concentrations above 100-200 mM (approximately 8-17 dSm^{-1}) (Wyn Jones et al., 1979; Greenway & Munns, 1980). Therefore, salt-tolerant plants growing under saline conditions must restrict the level of ions in the cytoplasm. As data above has illustrated, salt tolerant grasses utilize inorganic ions for a large part of their osmotic adjustment under saline growing conditions, as the ability to accumulate organic solutes on a whole cell basis is metabolically expensive, and therefore limited (Levitt, 1980; Kramer,1984). Salt tolerant plants that successfully accumulate saline ions for osmotic adjustment above concentrations of 100-200 mM do so by compartmentalizing them within the vacuole, which typically makes up 90 to 95% of mature plant cell volume (Flowers, 1985). Evidence exists for salinity inducing a K^+/Na^+ exchange across the tonoplast mediated by Na^+/H^+ antiport activity, resulting in saline ion compartmentation in vacuoles (Jeschke, 1984; Garbarino & Dupont, 1988). Under these conditions, osmotic potential of the cytoplasm is maintained by the accumulation of organic solutes that are compatible with enzyme activity, termed "compatible solutes" (Wyn Jones & Gorham, 1983; Wyn Jones, 1984). Under highly saline conditions, relatively few organic solutes, including glycinebetaine, proline, and certain polyols and cyclitols, can be accumulated in sufficient concentrations to osmotically adjust the cytoplasm without inhibiting enzymes (Gorham, 1996). Evidence exists for the cytoplasmic localization of these compounds (Leigh et al., 1981; Aspinall & Paleg, 1981; Wyn Jones, 1984). Of these, glycinebetaine and proline typically accumulate in grasses (Rhodes & Hanson, 1993).

Total leaf Na^+ + $Chloride^-$ levels exceeded 200 mM in all three Chloridoid grasses grown under moderate to high salinity (Figure 2), necessitating vacuolar ion compartmentation for survival. Glycinebetaine levels increased under salinity in all grasses, reaching highest levels (62 mM) in *Distichlis* (Table 3).

Table 3. *Leaf sap glycinebetaine and proline levels (mM) of grasses exposed to 0 and 300 mM Na Chloride.*

	Glycinebetaine		*Proline*	
Grass	*0 mM*	*300 mM*	*0 mM*	*300 mM*
Distichlis	12	62	1	2
S. virginicus	36	60	1	2
Zoysia	51	13	7	1
S. airoides	50	14	1	1
Cynodon	38	6	3	1
S. cryptandrus	36	13	3	1
Buchlon	20	8	6	2
Bouteloua	12	4	6	1
$LSD_{0.05}$	8	5	2	N.S.

Though proline concentrations also increased under salinity, maximum levels occurred in salt-sensitive BuchloN, reaching only 6 mM. Assuming that glycinebetaine and proline are located in the cytoplasm (see above), which occupies 10% of total cell volume, the contributions of glycinebetaine and proline to cytoplasmic osmotic adjustment can be calculated (Table 4). Glycinebetaine made substantial contributions to cytoplasmic osmotic adjustment in salt tolerant grasses only. In contrast, proline contributions were insignificant in all grasses.

Table 4.*Estimated[a] contribution to cytoplasmic osmotic adjustment of glycinebetaine and proline, in mosmol kg^{-1} (Osml), and as a percentage (%) of total osmolality, of plants grown at 300 mM Na Chloride.*

	Glycinebetaine		*Proline*	
Grass	*Osml*	*%*	*Osml*	*%*
S. virginicus	822	80	31	3
Distichlis	625	74	17	2
S. airoides	501	53	7	1
Zoysia	513	47	67	6
Cynodon	378	39	27	3
S. cryptandrus	357	18	29	1
Buchlon	209	10	59	3
Bouteloua	125	4	56	2

[a]*Estimate assumes glycinebetaine and proline are located in the cytoplasm, comprising 10 percent of total cell volume, with an osmotic coefficient of 1.0 for each compound.*

In another study, glycinebetaine made substantial contributions to cytoplasmic osmotic adjustment in 5 of 6 grasses in the study, the exception being salt-sensitive *Eremochloa ophiuroides* (Munro) Hack. The 5 salt tolerant grasses included *Cynodon*, *Zoysia*, and *Paspalum vaginatum* Swartz. As above, proline contributions

were too small to contribute to cytoplasmic osmotic adjustment (Marcum & Murdoch, 1994). Other studies involving *S. virginicus* support the importance of glycinebetaine as a compatible solute, relative to proline. Quaternary ammonium compounds (predominately glycinebetaine, and possibly other related betaines) accumulated to 48 μmol g^{-1} dry weight in shoots of *S. virginicus* grown in seawater, while proline levels reached only 1.6 μmol g^{-1} dry weight (Blits & Gallagher, 1991). Similarly, proline levels were insufficient to contribute significantly to cytoplasmic adjustment of *S. virginicus* grown in 80% seawater (Naidoo & Naidoo, 1998). In lines of tall wheatgrass grown under 20 dS m^{-1} total salinity, glycinebetaine accumulated to 45 μmol g^{-1} fresh weight in shoots, compared to only 1 μmol for proline (Weimberg & Shannon, 1988).

While glycinebetaine concentrations under salinity were positively correlated ($r^2 = 0.6$) with salinity tolerance among these eight grasses, proline concentrations were negatively correlated ($r^2 = -0.72$), suggesting that glycinebetaine, but not proline, acts as a compatible solute. Though both compounds have traditionally been considered compatible solutes, recent evidence has favored the role of glycinebetaine. For example, (i) glycinebetaine is excluded from the hydration sphere of enzyme proteins and thus tends to stabilize their tertiary structure (Yancy, 1994), (ii) corn (*Zea mays* L.) mutants lacking a critical enzyme for glycinebetaine biosynthesis also lack salt tolerance (Saneoka et al., 1995), and (iii) exogenously applied glycinebetaine has enhanced the salinity tolerance of glycophytes such as rice (*Oryza sativa* L.) (Harinasut et al., 1995). In contrast, proline accumulation has recently been considered by some investigators merely a result of plant injury, due to a universally rapid appearance following any type of stress (Colmer et al., 1995; Mumtaz et al., 1995).

2. SUMMARY

The Poaceae, represented by over 7,500 species, show extreme range in salinity tolerance, from salt-sensitive to extremely salt-tolerant (halophytic). In this chapter the range of salinity tolerance, and physiological adaptations to salinity present in grasses was described, focusing on eight grass species representing the range of salt tolerance present in the Poaceae. Salinity tolerance, indicated by 50% growth reduction, ranged from 150 mM in *Bouteloua* to >600 mM (seawater is approx. 550 mM) in *Distichlis* and *S. virginicus*. Though shoot growth decline with increasing salinity is typical, shoot growth may be stimulated by moderate salinity in highly salt-tolerant or halophytic grasses. However, root growth stimulation under moderate salinity is much more common in salt-tolerant grasses, resulting in increased root/shoot ratios, and therefore increased water absorption/transpiration area, which may be an adaptive mechanism to saline osmotic stress.

It has long been accepted that the major causes of plant growth inhibition under salinity stress are osmotic stress (osmotic inhibition of plant water absorption), and specific ion effects, including toxicities and imbalances. In a number of studies

salinity tolerance in the Poaceae has been related to shoot saline ion exclusion. However, studies have shown that complete osmotic adjustment does occur under salt stress, even in salt-sensitive grasses. Since the predominant osmotica utilized are typically saline ions, ion regulation, rather than ion exclusion, may be a more apt description of the mechanism of salt tolerance occurring in the Poaceae. Grasses regulate saline ion concentrations by vacuolar ion compartmentation at the root or shoot or by excretion via specialized salt glands, though ion reabsorption by xylem/phloem and redistribution to roots or senescing leaves may play a minor role.

Bicellular leaf epidermal salt glands occur in a number of C_4 grasses. Basal cells have specific ultrastructural modifications, including parallel partitioning membranes, allowing active, selective saline ion excretion. Excretion rates, which may be substantial, are dependent on media salinity level, and are typically highly selective for Na^+ and Cl^-. More recently, salinity tolerance of grasses has been related to salt gland excretion rate and leaf salt gland density.

Enzymes of higher plants, salt-sensitive and tolerant alike, are inhibited by saline ion concentrations above 100-200 mM. Under salt stress, grasses typically accumulate saline ions to well above these levels for shoot osmotic adjustment, necessitating Na^+ and Cl^- compartmentation in vacuoles, which comprise 90-95% of mature cell volume. Remaining cytoplasmic osmotic adjustment is achieved by certain organic osmotica compatible with cell enzymes, termed "compatible solutes". Glycinebetaine and proline typically accumulate in salt-stressed grasses, and have been proposed as compatible solutes. However, recent evidence has supported glycinebetaine, not proline, as a functional compatible solute.

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