EVAPOTRANSPIRATION EFFECTS ON SALT RELATIONS OF *LEPTOCHLOA FUSCA* (KALLAR GRASS)

by

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DEDICATED TO

MY PARENTS

The thesis submitted by Mr. Mohammad Arshad in partial fulfilment of the Degree of Master of Philosophy in the Department of Biological Sciences, Quaid-i-Azam University, Islamabad, is found satisfactory and is recommended for the award of the degree.

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ABSTRACT

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Studies were conducted to characterise Na^+ and Cl^- extrusion by the leaves of 'Kallar' grass subjected to various moisture levels and an antitranspirant (PMA). PMA decreased the transpiration rates of 'Kallar' grass leaves substantially 24 hours after application. Seventy-two hours after its application some decrease in the transpiration rates was observed, though differences between the treated and non-treated plants were small. Increasing NaCl caused reduction in transpiration rate at field capacity, and water deficit both in (PMA) treated and non-treated plants. However, reduction in transpiration with increasing NaCl in the medium was not apparent at flooding. In general, relative water contents were substantially decreased in NaCl treatments. At flooding, application of antitranspirant (PMA) slightly decreased the dry weights of tops at both salt levels. This decrease

in dry weights was also observed in plants at field capacity and water deficit. Application of PMA did not seem to have substantial effect on the extrusion of Na^+ and Cl^- by the 'Kallar' grass leaves. The absolute amounts of Na^+ and Cl^- extruded by the leaves substantially increased at hours 72 with increasing NaCl in the medium at flooding and field capacity. However, this trend was reversed at water deficit. Low availability of water may have affected the transport of salt to the leaves thus affecting extrusion.

INTRODUCTION

INTRODUCTION

Leptochloa fusca (Linn.) Kunth previously known as *Diplachne fusca* and known in Pakistan as 'Kallar' grass is a highly salt tolerant plant and grows well on saline sodic soil in the country. It is an annual plant which grows profusely during the period of July to September, which comprises Monsoon months, characterized by high rains and low transpiration. Work conducted on salt relation of 'Kallar' grass by the Plant Physiology Group of NIAB showed that the plant absorbed substantial amounts of K^+ compared with those of Na^+ from substrate containing low amount of K^+, but high of Na^+ (Bhatti et al., 1983). This high K^+ uptake was related to partial replacement of Na^+ and to the selective absorption of K^+. Over the range of NaCl concentrations used, Na^+ appeared to have little or no interaction with K^+ and no antagonism was apparent between Na^+ and K^+.

In time sequence studies on NaCl uptake by 'Kallar' grass net uptake of NaCl over the range of concentrations studies was not proportionate with the NaCl applied. Accordingly the occurrence of growth suppression and toxicity symptoms in the plants at moderately high NaCl may have been alleviated, in part at least, by the substantial extrusion of ions by the leaves (Bhatti and Wieneke, 1984b). Saturation in cellular absorption in the roots may have been reached early, leading to the restriction of salt uptake. While tissue concentrations increased progressively from hours 6 to 144, the net transfer rates for Na^+ and Cl^- were reduced in low salinity from hours 6 onwards. Whereas, in high salinity they increased slightly till hours 24, then remained fairly constant. In 'Kallar' grass the rate of uptake of Na^+ and Cl^- may have been limited by certain factors e.g., saturation, root efflux, or in part, to absorption of non-radioactive Na^+ and Cl^- during osmotic adjustment.

In subsequent studies on 'Kallar' grass tolerance of the plants to NaCl was related to preventing the tissue from accumulating high concentration by extrusion of both Na^+ and Cl^- by the leaves and their efflux by the roots, in addition to an equivalent retention in the leaf sheath.

To test the nature of salt deposits on the leaves, strips of cellulose tape were pressed against the upper and lower surfaces of the 4th leaves in 100 mM $^{22}NaCl$ and $Na^{36}Cl$ which were then autoradiographed. The autoradiograph of the cellulose tapes used to collect salt deposits from the surface of 4th leaf of plants grown in 100 mM $^{22}NaCl$ or $Na^{36}Cl$ suggested that excess salts were extruded both from the lower surface as well as from the upper surface. Leaves of the plants grown in presence of low NaCl extruded Na^+ and Cl^- in much the same way as those in high NaCl and the extrusion had already started after 6 hours of exposure to low salinity. Extrusion in 'Kallar' grass seemed, therefore, not to be specific to high concentration of Na^+ and Cl^- in the leaf tissue (Bhatti and Wieneke, 1984b).

To define the nature of extrusion it was, therefore, planned to follow salt absorption by 'Kallar' grass and the extrusion of salt by the leaves in relation to effects of phenylmercuric acetate, an antitranspirant on the leaves of plants grown in NaCl at various moisture levels in the soil.

REVIEW OF LITERATURE

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PLANT GROWTH AND SALT RELATIONS

(a) Effects of Substrate Salinity

Bhatti et al. (1983) studied the effects of NaCl, KCl, and $CaCl_2$ alone, and in combination of NaCl/KCl and NaCl/$CaCl_2$ on growth and ion uptake by 'Kallar' grass. They observed that NaCl and KCl had little effect on growth while $CaCl_2$ depressed the growth strongly. Concentration of Na^+ in the shoot exceeded those in the roots indicating the absence of retention mechanism in the roots. There was no interaction between Na^+ and K^+ or Na^+ and Ca^{2+}. On the contrary NaCl in two species of Agropyron depressed Ca^{2+} uptake. Elzam and Epstein (1969) reported the salt relation of two grass species, fall wheat grass (*Agropyron elongatum*) and intermediate wheat grass (*A. intermedium*). These were grown in nutrient solutions containing NaCl concentrations ranging from nil to 500 mM. It was observed that *A. elongatum* suffered damage at 100 mM and *A. intermedium* at 5 mM. They concluded that severe effect of NaCl on growth were correlated with extremely low level of Ca^{2+} in the roots. Tissues of tops and roots in 'Kallar' grass showed strong selectivity for K^+ over Na^+. Suggestion for selective K^+ uptake by 'Kallar' grass tops was also made by Sandhu et al. (1981) who observed that the concentration of Na^+ in the leaf washes of plants in high NaCl exceeded those of K^+, Ca^{2+} and Mg^{2+}. Thus they proposed that extrusion of Na^+ was selective. However, the growth of the plant in the treatment was highly suppressed which renders the conclusion invalid. Presence of salt glands on the leaves of 'Kallar' grass was reported by Joshi et al. (1983) and the presence of pore in each gland suggested that salts are excreted through these pores. The excretion of salt was highly selective for Na^+ and Cl^-. The glands also excreted K^+, Ca^{2+} and Mg^{2+}. The order of preference regarding cation excretion was found to be $Na^+ > K^+ > Ca^{2+} > Mg^{2+}$.

Bhatti and Wieneke (1984a) studied leaf extrusion, retranslocation and root efflux in *Diplachne fusca* (Kallar grass) grown in NaCl. On the basis of specific activity, the distribution of Na^+ and Cl^- in the tissue was followed during and after treatment. Sequential collection of leaf washes showed that both Na^+ and Cl^- were extruded at a somewhat constant rate. They also reported that the leaf sheaths accumulated more Na^+ and Cl^- than the leaf blades. The concentration of various ions in the extruded salt were Na^+ 40.5, Cl^- 36.8, K^+ 0.72, Ca^{2+} 0.68 and Mg^{2+} 0.22 μmoles/plant. Clearly, Na^+ ions predominated other ions i.e., Cl^-, K^+, Ca^{2+} and Mg^{2+} in extrusion. However, in time sequence studies on uptake and distribution of Na^+ in *Diplachne fusca* grown in NaCl showed (Bhatti and Wieneke, 1984b) that increasing NaCl raised the concentrations of Na^+ and Cl^- in the tissues of tops and roots but had little or no effect on plant growth. They reported that young and old leaves extruded 30-60% and 30-70% respectively of their total Na^+ and Cl^- absorbed. According to their statement as the amounts of Na^+ and Cl^- in the tissue increased with time, their extrusion also increased, however, as a proportion of the total Na^+ and Cl^- it did not change much with time. They autoradiographically showed that the extruded salts were distributed equally on the upper and lower surface of all leaves, parallel to veins. There seemed to be a more intense distribution of Na^+ and Cl^- in the leaf sheaths as well as in the apical region of roots. Although Na^+ ions exceeded the concentrations of K^+,

Ca^{2+} and Mg^{2+}, the authors suggest that the extrusion process was not specific to high NaCl in the substrate.

Salt Secretion: Scholander *et al.* (1962) studied the various parameters of the salt balance in several species of mangroves and concluded that the salt concentration in the excreted fluid was often higher than that of seawater and salt secretion was an active process and it was not related to transpiration stream.

Pollak and Waisel (1970) worked on ecophysiology of salt tolerance in *Aeluropus litoralis* and the effect of external NaCl concentrations on ion excretion was examined using detached leaves. Excretion was positively correlated with the external NaCl concentration upto the concentration range of 0.2-0.4 M in which the leaves reached their highest excretion capacity. Excretion decreased beyond this range. On the other hand, Na^{+} content of the leaves increased with the increase in external concentration upto concentration of 0.6 M. They also studied the effect of low and high humidity on salt excretion process and found that when leaves were exposed to dry atmosphere, salt excretion was reduced by the high external NaCl concentration. But under humid conditions absolute excretion increased.

Such enhancement is attributed to the increase of salt transport via transpiration stream.

Characteristics of salt secreted by *Tamarix aphylla* were studied by Berry (1970). He determined the composition and concentration of salts secreted by the salt glands of *Tamarix aphylla* (Linn.) grown under controlled nutrient conditions. Eight ions, Na, K, Mg, Ca, Cl, NO_3, HCO_3 and SO_4, constituted 99% of the dry weight of salts secreted by plants grown on half-strength Hogland's solution. The bivalent cations Mg and Ca accounted for most of the cations; HCO_3 comprised about 60% of the anions. The micro-nutrients B, Mn, Cu, Zn and Mo were present in enriched concentrations in the secretion. The composition of the secretions was highly dependent on the composition of the root environment. The predominating cation in the saline culture solutions was also the predominant cation secreted. The accompanying anion in the culture solution influenced the cation composition of the secreted salt. The concentration of the salt gland secretion averaged 0.5N, a 50-fold increase in concentration over the nutrient solution in which the plants were grown.

The secretion of ions from salt glands and the salt content of *Sporobolus arenarius* leaves were investigated by Ramati et al. (1976). They observed that the NaCl concentration of the test solution was positively correlated with that of the secreted fluid and of the leaves. Electron probe analysis revealed different contents of sodium potassium and chloride in mesophyll and gland cells. They have also proved that the secretion of salts by salt glands is an active process.

Bennert et al. (1983) investigated salt secretion of *Atriplex hymenelytra* and estimated the fraction of secreted salts. They also observed that 1/3 - 3/4 of osmotically active compounds were deposited as a salt on the outer leaf surface depending on season and leaf age. Analysis of inorganic (Na^+, K^+, Cl^-) and organic (oxalate) ions in the total leaf material and secreted salt layer showed Na^+ as dominating cation and Cl^- was present in much less than equiomolar concentration.

Walker et al. (1984) studied anatomy, ultra structure and assimilate concentration of roots of citrus genotypes differing in ability for salt exclusion. Seedlings of *Citrus reticulata* and *C. medica* treated in water culture with 0, 25, 50 and 100 mol m^{-3} NaCl and in sand culture with

0 and 100 mol m^{-3} NaCl, leaf analysis for Cl^- indicated that C. *medica* accumulated the most chloride at all levels of salinity. Chloride concentration increased with salt treatments.

(b) Transpiration Effects

Oertli (1965) observed the effect of external salt concentrations on water relations in plants and concluded that under saline conditions an osmotic adjustment of the root xylem sap is unlikely and consequently, the rate of water uptake should be reduced. Under saline conditions and under non-osmotic soil moisture stress, a higher osmotic differential between leaf vacuoles and immediate surroundings is required for turgidity. Growth reduction may result, if leaves cannot fully cope with this requirement.

Influence of water and salt stress on water relationships and CO_2 exchange of tops and roots in beans was observed by Jensen (1981). He suggested that when low-salt plants grown in nutrient solution, were exposed to osmotic potentials in the root medium of -2.7 and -4.7 bar due to the addition of KNO_3, osmotic adjustment occurred. The leaf osmotic potential (OP) decreased, leaf turgor potential and leaf water content were maintained, no wilting took place, stomatal conductance was partially regained and net photosynethsis was only moderately depressed. When low-salt plants were exposed to osmotic potential -2.7 and -4.7 bar due to the addition of polyethyleneglycol 1500, no adjustment to water stress was observed. As the turgor potential decreased, the leaves became dehydrated and high percentage wilted. Stomatal conductance, net photosynthesis, top dark respiration and root respiration were depressed. Nitrate uptake ceased completely at -4.7 bar. When low salt plants were exposed to osmotdic potential -4.7 bar, due to both polyethleneglycol (-2 bar) and KNO_3 (-2 bar) osmotic adjustment took place: osmotic potential of the leaves decreased, leaf water contents, turgor potential stomatal conductance, net photosynthesis, top dark respiration and root respiration recovered to some extent, but the proportion of wilted leaves was high. When medium and high salt plants, osmotically adjusted to osmotic potential -2.7 and -4.7 bar due to KNO_3, which were exposed to water stress due to polyethyleneglycol (-2 and -4 bar), turgor potential and leaf water content were maintained, none or few leaves wilted and stomatal conductance was depressed less than in low-salt plants. These responses are attributed to influence of pre-osmotic adjustment on turgor maintenance and hydration of the plant. It is concluded that osmotic adjustment by inorganic solute uptake, before or during exposure to water and salt stress, can reduce the severe effect of low water and salt stress and can reduce the severe effects of low water potentials in the root medium.

Growth of *Atriplex halimus* in NaCl salinized culture solution as affected by the relative humidity of the air, was studied by Gale et al. (1970). They found that small amounts of NaCl were needed by *A. halimus* in order to overcome the stress caused by low relative humidity of the air. They also observed that salinity was harmful to growth at all concentrations under low evaporative conditions.

Malash and Flowers (1984) elucidated the effect of antitranspirant phenylmercuric acetate (PMA) on salt tolerance in wheat and observed that PMA reduced the growth under non-saline conditions, this was reflected in a reduced leaf area. However, low (50 μM) and medium (100 μM) concentrations of PMA under saline condition increased plant dry weights and leaf area per plant when compared with the saline control (no PMA). PMA treatment lowered shoot sodium and chloride content. Selectivity for K^+ over Na^+ was consequently enhanced by PMA. So PMA applications at a suitable concentration can improve growth under stressed conditions (salinity) via its effect on the plant water balance, decreased salt content and increased leaf area for photosynthesis. However, continued PMA applications to the plant had an accumulative toxic effect, and under non-stressed conditions decreased growth of plants by reducing photosynthesis, because plants did not benefit from stomatal closure enough to offset the injury caused by PMA.

Boobathi and Singh (1984) worked on transpiration suppressants on spring sorghum (*Sorghum bicolor*) in relation to soil moisture regime, and effect on growth and nutrient uptake. They observed that in crop growth, measured by plant height, leaf area index, dry matter production and uptake of Na, P and K increased with more frequent irrigation and response to spraying of transpiration suppressant. Foliar application of atrazine at 200 g/ha and chloromequat chloride (CCC) at 300 ml/ha gave the best results.

Biddulph et al. (1960) studied ascension of calcium in relation to transpiration stream and reported the time course curve for Ca^{45} entry into specific stem sections and concluded that entrance consisted of two phases: a reversible exchange phase and an irreversible accumulation phase. The exchange phase was complete in 3 hours and the exchangeable fraction constituted less than 10% of the total calcium. But in contrast Hill (1967) studied the ion and water transport in *Limonium vulgare* and found that the application of Nernst equlibrium equation to the transport of ions in the leaf gland cells of *Limonium vulgare* indicated that Na^+, K^+ and Cl^- were actively transported out of the cells. In contrast two different variations in the culture solutions of *Tamarix aphylla* were used by Berry and Thomson (1967). The salt obtained from the glands of plants growing in the culture solution in which the sodium concentration was increased to 16 meq Na^+/ℓ showed an increase in sodium and decrease in potassium in the secreted salt. The composition of the secreted salt was apparently a function of the composition of the root environment, and no apparent selectivity for sodium over potassium was noted.

MATERIALS AND METHODS

MATERIALS AND METHODS

Nodes of *Leptochloa fusca* (Linn.) Kunth ('Kallar' grass stems were collected from the experimental field of Biosaline Research Sub Station (BSRS), Lahore of Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad, for studies on evapotranspiration effects on salt relations of 'Kallar' grass.

PLANT CULTURE AND TREATMENTS

The experiment was conducted in the Plant Physiology Laboratory of Soil Science Division of NIAB, Faisalabad. Pots (60) were filled with 1500 gm Thikriwala (Faisalabad) soil (clay = 6.8%, silt = 10.50%, sand = 82.7%, Ec_e = 2.2 $mScm^{-1}$ Bhatti et al., 1983). The soil was divided into two portions, 500 and 1000 g. A plastic sheet was placed between the 500 upper and 1000 gm the lower soil in pots. Plants were raised from sets of nodes of 'Kallar' grass sown in the upper 500 gm soil which was moistened to field capacity with deionized water. Nitrogen and phosphorus were added to the soil as basal nutrients in the form of solution at the rate of 60 kg/ha as urea and 40 kg P_2O_5/ha as $NH_4H_2PO_4$. At 55th day of sowing the number of plant per pot was thinned to five. On 63rd day, the leaves were washed with distilled water to remove dust and salt particles and the salt treatments were applied in triplicate as 300 ml solution containing 10 and 300 mM NaCl/ℓ to the main body of the soil (1000 gm). The plants were exposed to the treated soil by removing the intervening plastic sheet. In soil different moisture levels i.e., flooding, field capacity and water deficit were maintained with deionized water. Thereafter, the soil moisture was kept constant by adding the amount of water lost. Plants in half of the pots were treated with phenylmercuric acetate (PMA) by sparying both surfaces of the leaves with solution containing 0.1 mM PMA in 0.2% aqueous solution of Ola (wetting agent).

TRANSPIRATION RATES

After 72 hours of treatment with PMA, transpiration rate of the plants in 12 pots from all the treatments (of which 6 were sprayed with antitranspirant, PMA) was measured by rapid weighing method (Franco and Magalhaes, 1965). Five leaves one from each plant were excised from each pot and their cut ends were covered with parafilm in order to avoid water loss. The leaves were hung with the hook of a balance (Mettler Model H-300) from the end covered with parafilm and were immediately weighed for fresh weight with the windows of balance closed. The windows were then opened to allow the air to cross. Two minutes after, the leaves were weighed again but with the windows closed. In all, five observations were made each after two minutes interval using the above procedure.

RELATIVE WATER CONTENT

Immediately after weighing the leaves from all the treatments were kept at room temperature (34°C) for three hours with cut ends submerged in water in beakers including one hour in cold water (5°C). The leaves were removed from the beaker, dried between the folds of tissue paper and weighed for fresh weights when they were fully turgid. Finally, the leaves were dried in oven at 72°C for 24 hours and their dry weights determined.

LEAF WASHING

At 24 hours after salt treatment of plants, the leaves of plants in 24 pots which were subjected to high salt treatment (300 mM NaCl) were washed with equal quantities of distilled water and washes (W_1) of the leaf blades and the leaf sheaths were collected. Similarly at 72 hours and 144 hours after salt treatment the leaves of the plants were washed and the washes (W_2, 36 pots) and W_3 (12 pots) respectively were collected. Washing of the intact growing leaves was done by enclosing the tops carefully in polythene bag and by spraying the leaves in the bag with atomized water. The pots were tilted to keep the plant tops somewhat downward during the spraying procedure. The plants were finally shaken to remove droplets from the leaves.

HARVEST

The plants in 48 pots were harvested and fresh weights of the above ground parts were taken. At harvest the roots were given a quick rinse under the running tap water and washed in deionized water each for three minutes to remove any ion adsorbed at root surfaces. The cluster of roots were then dried between the folds of tissue papers each for one minute in order to remove surplus water and fresh weights were taken. The roots and tops were then dried in oven at 72°C for 24 hours. After that, the leaf blades were separated from the leaf sheath and dry weights of all the parts of plants were taken separately.

DRY ASHING AND ANALYSIS

All the parts of plants were cut into fine pieces separately. Parts of plant material were taken and CaO was added at the rate of ¼th of plant material (Chapman and Pratt, 1961) to avoid losses of ions during dry ashing. Then little amount of distilled water was added to wet the plant material and put into Karl Kolb muffle furnace (Model L-47-T) at 500°C for three hours. The dry ashed plant materials were dissolved in 0.5 N HNO_3 (Jackson, 1958). The dissolved materials were analysed for Na^+ and K^+ using flamephotometer Model 69 Karl Kolb and for Cl^- using Corning chloride meter Model 920.

RESULTS

RESULTS

(A) TRANSPIRATION AND RELATIVE WATER CONTENT

PMA application to the leaves of 'Kallar' grass decreased the transpiration rates substantially at 24 hours after its application in the field (BSRS, Appendix I). Seventy two hours after application of anti-transpirant (PMA) to the leaves of experimental plants grown in the laboratory, caused some decrease in transpiration rates (Table 1): the differences between treated and non-treated plants were however, small. Increasing salinity of the medium caused reduction in transpiration at field capacity and water deficit both in the PMA treated, and non-treated leaves. However, reduction in transpiration with increasing NaCl of the medium was not apparent at flooding. Relative water contents were higher at flooding than those at field capacity and water deficit. In general, relative water

TABLE 1

Effect of PMA on transpiration rates and relative water contents of excised leaves of 'Kallar' grass grown at the two concentrations of NaCl at various levels of moisture in soil.

(72 hours after treatments)

Treatments	NaCl (mM)	-PMA		+PMA	
		Transpiration rate μℓ/min/g	Relative water content (%)	Transpiration rate μℓ/min/g	Relative water content (%)
Flooding	10	5.7427	94.16	5.4275	89.72
	300	5.6789	98.88	5.5191	87.92
Field capacity	10	4.9696	88.32	4.5397	80.80
	300	3.3946	82.82	3.1923	73.64
Water deficit	10	4.9460	81.89	4.8397	70.65
	300	3.1656	85.16	3.0121	83.11

contents were substantially decreased in NaCl treatments.

(B) GROWTH

Dry Weight

Application of antitranspirant (PMA) slightly decreased the dry weights of the tops at both salt levels at flooding (Table 2). This decrease in dry weights was also observed in plants at field capacity and water deficit, at low salt level (10 mM NaCl/l). PMA application also decreased the dry weights of the roots generally, though, the differences between plus and minus PMA were small.

The dry weights of the tops and the roots of 'Kallar' grass plants in 10 and 300 mM NaCl were higher at flooding than at field capacity and water deficit. This increase in dry weights was more pronounced in the roots than in the tops (Table 2). Increasing concentration of NaCl in the medium from 10 to 300 mM depressed the dry weights at field capacity and water deficit but the weights were little affected at flooding.

TABLE 2

Effect of Phenylmercuric acetate (PMA) on dry weights of tops and roots of 'Kallar' grass grown at two concentrations of NaCl at various levels of moisture in the soil

(dry weight: mg/plant)

Treatments	NaCl (mM)	-PMA		+PMA	
		Tops	Roots	Tops	Roots
Flooding	10	260.68 ± 57.5	182.86 ± 21.6	232.38 ± 62.99	121.24 ± 22.9
	300	260.32 ± 57.5	97.08 ± 1.7	200.72 ± 15.92	97.42 ± 9.2
Field capacity	10	232.74 ± 56.5	95.4 ± 27.4	229.82 ± 1.55	89.46 ± 19.6
	300	202.74 ± 44.5	94.42 ± 7.4	173.46 ± 37.87	79.06 ± 8.3
Water deficit	10	231.40 ± 11.4	92.72 ± 2.4	192.68 ± 12.55	69.66 ± 4.7
	300	200.72 ± 15.4	87.40 ± 3.4	202.42 ± 55.79	77.22 ± 8.0

(C) EXTRUSION BY LEAVES

Na^+, Cl^- and K^+

The amounts of Na^+ and Cl^- extruded as percentage of total plant contents in leaves treated with PMA, were, in general, similar to those in the leaves that were not treated with PMA, both at 72 and 144 hours following treatment (Table 4 and 5). The amounts extruded at 72 and 144 hours were, however, significantly higher than those at 24 hours (Table 3). The amounts of K^+ extruded by PMA treated, and non-treated leaves varied slightly from each other both at 72 and 144 hours, but the values showed fair resemblance (Table 6). However, K^+ extrusion both at 72 and 144 hours was much below that of Na^+ and Cl^-.

The amounts of Na^+, K^+, and Cl^- extruded by 'Kallar' grass leaves at 24 hours following treatment with 300 mM NaCl were more or less similar at all moisture levels i.e., flooding, field capacity and water deficit (Table 3).

At 10 mM NaCl, absolute amounts of Na^+ and Cl^- extruded by the plant leaves were generally similar at field capacity and water deficit, but they were substantially lower at flooding.

TABLE 3

Concentration of Na^+, K^+ and Cl^- in the leaf washes of 'Kallar' grass 24 hours after treatment with 300 mM NaCl at various levels of moisture in the soil.

(concentrations: mM/plant)

Treatments	Na^+	K^+	Cl^-
Flooding	5.84	2.34	5.22
Field capacity	6.86	2.78	5.36
Water deficit	5.98	2.67	6.85

TABLE 4

Effect of Phenylmercuric acetate (PMA) on the concentration of Na^+ in the leaf washes, the blades, the sheaths and the roots of 'Kallar' grass plants grown at two concentrations of NaCl at various moisture levels in the soil.

(Na^+ in mM/plant)

Treatments	NaCl (mM)	-Phenylmercuric acetate						+Phenylmercuric acetate					
		Leaf washing	Tops		Roots	Total	Extrusion as % total contents	Leaf washing	Tops		Roots	Total	Extrusion as % total contents
			Blades	Sheaths					Blades	Sheaths			
At 72 hours													
Flooding	10	7.4	25.9	14.3	25.5	73.0	10.1	6.8	24.0	16.4	14.9	62.0	10.9
	300	15.2	32.9	18.0	24.2	75.2	20.2	9.6	21.7	13.4	21.2	65.9	14.6
Field capacity	10	19.0	33.0	22.3	14.9	89.1	21.3	22.4	35.7	17.8	14.0	89.9	24.9
	300	29.2	40.5	24.9	28.4	93.7	31.1	39.0	32.4	21.9	26.7	120.0	32.5
Water deficit	10	13.7	24.2	16.9	12.2	66.9	20.5	11.5	13.7	12.9	9.0	47.0	24.4
	300	5.5	25.0	21.7	24.5	75.8	7.2	8.2	22.7	25.5	23.8	80.2	10.2
At 144 hours													
Flooding	10	12.7	27.2	11.2	11.3	62.4	20.3	10.8	30.2	14.6	16.5	72.1	15.0
	300	27.4	47.0	21.5	16.5	112.4	24.5	32.0	48.7	23.5	18.7	123.7	26.5

TABLE 5

Effect of Phenylmercuric acetate (PMA) on the concentration of Cl^- in the leaf washes, the blades, the sheaths and the roots of 'Kallar' grass plants grown at two concentrations of NaCl at various levels of moisture in the soil.

(Cl^- mM/plant)

Treatments	NaCl (mM)	-Phenylmercuric acetate						+Phenylmercuric acetate					
		Leaf washing	Tops		Roots	Total	Extrusion as % total contents	Leaf washing	Tops		Roots	Total	Extrusion as % total contents
			Blades	Sheaths					Blades	Sheaths			
At 72 hours													
Flooding	10	10.4	34.9	16.4	26.4	88.0	11.8	8.4	26.0	32.0	17.3	83.8	10.0
	300	15.8	48.8	39.4	15.5	119.5	13.0	15.5	27.1	35.3	17.5	95.3	16.3
Field capacity	10	18.4	31.7	27.1	9.0	86.2	21.3	20.1	20.0	36.1	18.9	95.1	21.2
	300	22.4	50.0	36.4	31.3	140.0	16.0	43.9	51.6	58.2	22.8	176.4	24.8
Water deficit	10	13.4	38.6	26.2	11.2	89.4	15.0	12.3	27.4	24.0	15.5	79.2	15.6
	300	4.8	28.3	41.4	20.9	95.4	5.0	7.4	34.2	40.0	16.7	98.4	7.6
At 144 hours													
Flooding	10	15.0	19.2	34.4	26.2	94.8	15.8	14.4	27.6	32.7	11.4	86.0	16.7
	300	27.1	91.7	37.3	14.1	170.2	15.9	34.0	99.6	29.3	20.9	183.9	18.5

TABLE 6

Effect of Phenylmercuric acetate (PMA) on the concentration of K^+ in the leaf washes, the blades, the sheaths and the roots of 'Kallar' grass grown at two concentrations of NaCl at various moisture levels in the soil.

(K^+ mM/plant)

Treatments	NaCl (mM)	-Phenylmercuric acetate						+Phenylmercuric acetate					
		Leaf washing	Tops		Roots	Total	Extrusion as % total contents	Leaf washing	Tops		Roots	Total	Extrusion as % total contents
			Blades	Sheaths					Blades	Sheaths			
						At 72 hours							
Flooding	10	3.0	48.0	17.3	70.2	138.6	2.2	3.2	36.7	19.6	35.7	95.2	3.32
	300	3.6	58.2	30.9	31.7	124.6	2.9	3.3	32.9	18.7	34.4	89.4	3.71
Field capacity	10	6.2	40.1	21.1	24.7	92.2	6.8	6.1	37.9	21.4	27.3	92.6	6.6
	300	4.1	38.0	18.0	27.7	87.9	4.7	6.6	30.3	16.4	21.8	75.0	8.8
Water deficit	10	4.3	43.1	21.5	27.1	96.0	4.5	3.7	30.6	19.4	16.5	70.3	5.3
	300	3.3	39.3	19.8	28.6	91.0	3.6	1.3	38.3	19.5	27.6	86.7	1.5
						At 144 hours							
Flooding	10	4.7	54.1	19.8	31.3	109.9	4.3	4.4	59.1	23.1	31.6	118.2	3.7
	300	4.6	41.6	14.9	22.9	84.0	5.5	5.9	53.4	17.0	31.1	107.5	5.5

The amounts of Na^+ and Cl^- extruded by the leaves of 'Kallar' grass increased at hours 72 when the salinity of the root medium was increased from 10 to 300 mM NaCl and the water level was maintained at flooding and field capacity (Tables 4 and 5). However, this trend was reversed when plants were kept at water deficit. Thus, the amounts of Na^+ and Cl^- extruded by the leaves decreased with an increase in the salinity of the medium. Low availability of water may have affected the transport of salt to the leaves, thus affecting extrusion.

Amount of Na^+ and Cl^- extruded during 72 hours of exposure to NaCl was generally higher at field capacity than at flooding and water deficit both under low and high salt levels (Tables 4 and 5).

With the increase in time interval from 72 to 144 hours the amount of Na^+ and Cl^- were substantially increased. Potassium extrusion from 'Kallar' grass leaves also increasd with time (from 72 to 144 hours) which was however, 1/5th that of Na^+ extrusion.

(D) Na^+, Cl^- AND K^+ AS PERCENT TOTAL PLANT CONTENTS

Na^+ extrusion as percentage of the total plant contents also increased with increasing levels of NaCl in the medium at flooding and field capacity (Table 4). However, at water deficit and high salt level (300 mM), NaCl extrusion capacity of the leaves was reduced to less than half of that at low salt level (10 mM).

Application of PMA apparently did not seem to affect Na^+ in the leaf washes, the leaf blades, the leaf sheaths and the roots at both levels of NaCl. Na^+ extrusion (%) apparently remained unaffected by the application of PMA.

Chloride extrusion (%) from leaves remained similar both at low (10 mM) and high (300 mM) NaCl levels at flooding and field capacity (Table 5). But at water deficit, salt extrusion capacity of the leaves decreased strongly with increase in the salinity of the medium. Cl^- extrusion percentage was similar at hours 144 both at low and high salt levels. Chloride contents in the leaf washes, the leaf blades the sheaths and the roots were little affected by the application of PMA.

K^+ extrusion (%) from the leaves was higher at field capacity than at flooding and water deficit at 10 mM

NaCl (Table 6). Potassium extrusion remained generally similar at low (10 mM) and high (300 mM) NaCl at flooding but decreased with increasing salt level at field capacity and at water deficit (72 hours). At flooding, K^+ extrusion (%) increased with time (144 hours). When salt level in the root medium was raised from 10 to 300 mM, the application of PMA gave small increase in K^+ content of the leaf washes while in the blades the concentrations in the treated plants were lower than those in the non-treated ones. However, the concentrations of K^+ in the leaf sheaths in both treated and non-treated plants were similar.

(E) TISSUE CONCENTRATIONS

Sodium

The concentration of Na^+ in various parts of PMA treated 'Kallar' grass plants were in general, similar to those plants which were not treated with PMA (Table 4).

The amount of Na^+ in the leaf blades increased when the salinity of the root medium was increased from 10 to 300 mM and the plants were kept at flooding and field capacity (Table 4). However, at water deficit, the Na^+ contents remained similar at both low and high NaCl concentratio

At flooding, Na^+ contents in the leaves at various times (72 and 144 hours after treatment) remained similar at 10 mM NaCl but increased at 300 mM NaCl (Table 4).

In the leaf sheath, Na^+ content increased with the increase in NaCl level in the root medium at flooding, field capacity and water deficit. At flooding, the amount of Na^+ in the roots remained similar at low and high NaCl levels but increased at field capacity and water deficit with increasing level of NaCl in the medium. Total amount of Na^+ per plant was higher at field capacity than at flooding and water deficit both at 10 and 300 mM NaCl treatments. At 72 hours after treatment, total Na^+ per plant increased slightly with increasing level of NaCl in the medium. However, total Na^+ per plant increased substantially with increased level of NaCl in the medium at hours 144 (Table 4).

Chlorides

The concentration of Cl^- in the various parts of PMA treated 'Kallar' grass plants was somewhat similar to that in the non-treated plants (Table 5).

The chloride contents in the leaf blades significantly increased when the NaCl level was increased from 10 to 300 mM at flooding and field capacity. But at water deficit amount of Cl^- decreased at higher salt level in the medium. At flooding Cl^- contents in the leaf blades increased with time from 72 to 144 hours following treatments at high NaCl level but this trend was not observed at low salt level (10 mM).

In the leaf sheath, chloride contents increased with the increase in NaCl level in the root medium at flooding, field capacity and water deficit at 72 hours following treatments. At flooding, Cl^- contents in the leaf sheaths at 144 hours following treatment were similar at low and high salt level (Table 5).

At 72 and 144 hours after treatments the amount of Cl^- in roots substantially decreased at 300 mM than at 10 mM NaCl level when the plants were kept at flooding. Significant increase in Cl^- contents was observed at high NaCl treatment both at field capacity and water deficit. Total amount of Cl^- per plant was higher at field capacity than at flooding and water deficit when the plants were grown at 300 mM NaCl. At 10 mM NaCl/l, total Cl^- per plant remained generally, similar at all water levels. However, at water deficit total Cl^- per plant was more or less similar at both salt levels. Total chloride contents per plant increased substantially with time (from 72 to 144 hours) at high salt level in the medium.

Potassium

K^+ concentration in various parts of PMA treated 'Kallar' grass plants were, in general, similar to those in the non-treated plants (Table 6).

The K^+ contents in the leaf blades slightly increased when the NaCl level was increased from 10 to 300 mM at flooding after 72 hours following treatment. However, at 144 hours K^+ contents decreased at high NaCl level.

At field capacity and water deficit, K^+ contents in the leaves were similar at both low and high NaCl treatments. In the leaf sheaths, K^+ contents increased with increase in NaCl level in the medium at flooding (72 hours following treatments). However, K^+ contents slightly decreased (at 144 hours) when salinity of the medium was raised.

At field capacity and water deficit, K^+ contents in the leaf sheaths were generally similar at low and high NaCl in the medium (Table 6).

At flooding, the K^+ contents in the roots decreased substantially at high than at low NaCl level. This decrease in K^+ contents at flooding was also observed at hours 144. At field capacity and water deficit, K^+ contents of the roots generally remained unaffected by increase in the salt level. Total K^+ contents per plant were higher at both salt levels than those at field capacity and water deficit (72 hours after treatment). However, it remained little affected by increase in salt level both at field capacity and water deficit. The total K^+ contents per plant decreased at hours 144 with increase in the salt level at flooding.

DISCUSSION

DISCUSSION

(A) GROWTH

In growth response to NaCl and flooding, 'Kallar' grass resembled the salt marsh plant, *Salicornia europa* which produced more dry weights at flooding in the presence of NaCl (Cooper, 1982). In *Salicornia europa* the positive response to the treatment was suggested to indicate that the plant required salts on waterlogged soil. In 'Kallar' grass water-logging alone also produced more growth than obtained at the field capacity in other experiments (Bhatti unpublished data). Rozeman and Blom (1977) demonstrated that in upper marsh species *Funcus gerardii* and *Agrostis stolonifera* water-logging caused a stimulation in iron and manganese uptake. Such an effect of salinity and flooding on the absorption of elements such as Zn, Cu and iron was not, however, shown in studies on 'Kallar' grass (Bhatti, unpublished data). A positive salinity-trace elements effect on growth has, however, been shown in corn elsewhere (Bhatti and Sarwar, 1977). Whether, the positive response to iron and manganese (*Salicornia europa*: Cooper, 1982), or Zn, and Cu (Corn: Bhatti and Sarwar, 1977) has a parallel in the growth of 'Kallar' grass is not known.

The depression caused by PMA on the dry weights of 'Kallar' grass in the presence of NaCl in the present experiment, however, is in contrast with the beneficial effects of PMA reported on wheat under saline conditions (Malash and Flowers, 1984). The ameliorative effect was attributed to increased photosynthetic area due to decreased NaCl uptake in the shoot, and to leaf longevity. Under condition of low water supplies, the ameliorative effects of PMA in increasing growth, and yield in other plants are also known (Davenport et al., 1972; Fuehring, 1973). Conversely, in some plants species (e.g., spring wheat: Brengle, 1968; Tomato: Mishra and Pradhan, 1972) PMA had adverse effects. However, the ameliorative effects of PMA were related to reduced Na^+ and Cl^- uptake, which may have arisen from suppression of the rate of uptake of ions carried by the transpiration stream.

Higher amounts of water lost from 'Kallar' grass under flooding than under field capacity or water deficits, and the rate of loss were related to the high water status of the plants i.e., high relative water content. Thus, the effect of waterlogging on growth could be related to the relative water contents (or turgor) in much the same way as the increased plant height of *Atriplex halimus* under humid conditions (Gale et al., 1970). Addition of NaCl, however, decreased growth of *Atriplex halimus* under these conditions. While PMA decreased growth in 'Kallar' grass, it also decreased rate of transpiration as well as relative water contents (Table 1). The effect of PMA however, diminished 24 hours after its application and the subsequent effects on growth could not be related to the initial effect of treatment on transpiration and relative water contents.

(B) SALT RELATIONS

Although the growth of 'Kallar' grass plants treated with phenylmercuric acetate (PMA) was markedly depressed 72 hours following its application, there was no effect on the absorption of Na^+ and Cl^- in the tissue, or on extrusion of Na^+ and Cl^- by the leaf blade. That the effect of PMA persisted for a period of 24 hours is supported by data on rate of transpiration and relative water content, for effects to continue further, the plant could be sprayed intermittently as was done by Malash and Flowers (1984). One would, then expect that following prolonged treatment there might be a strong depression in growth (Brengle, 1968; Mishra and Pradham, 1972) and Na^+ and Cl^- uptake (Malash and Flowers, 1984). Although no effect was demonstrated on uptake and on extrusion of Na^+ and Cl^- by leaf blade following initial treatment of plants with PMA, the effects on other parameters were however, confined only to the first 24 hours of its application. In absorption of Na^+ and Cl^-, 'Kallar' grass resembled *Armeria maritima* (Baumeister and Ziffus, 1981) since increasing application of NaCl increased uptake and extrusion. Whereas the effect of increasing application of NaCl on uptake and extrusion was obvious only at flooding and field capacity, the treatments, appeared, therefore, to be complementary in their effects i.e., increased moisture was required to affect uptake and extrusion.

An increased application of NaCl may have an accelerating effect on extrusion could be inferred from the observation that in 'Kallar' grass leaves exposed to higher NaCl (100 mM) in solution, the salt glands ruptured earlier than those in the low NaCl (10 mM) treatment (Bhatti et al., 1985). In other studies (Sandhu et al., 1981; Joshi et al,

1983) where Na^+ and Cl^- exceeded the concentration of K^+ in the leaf washes (Joshi et al., 1983) it was suggested that Na^+ and Cl^- were selectively extruded. Although, Na^+ predominated over other ions viz. K^+, Ca^{2+} and Mg^{2+} in various studies (Bhatti and Wieneke, 1984b; Bhatti et al., 1983) including the present one, the extrusion of Na^+ and Cl^- by the leaves of plants in the low NaCl (10 mM) treatment (Bhatti and Wieneke, 1984b) does not seem to be in keeping with the thought (Sandhu et al., 1981; Joshi et al., 1983) that Na^+ and Cl^- were selectively extruded. That the increased extrusion of Na^+ and Cl^- seems to be related to the amounts of moisture in the substrate asks for further investigations. Possibly K^+ and Cl^- are accumulated in the vacuoles of the leaf cells vis-a-vis the bulk of Na^+ that may have been retained in the extracellular regions (and possibly cytoplasm: cf. Waisel and Eshel, 1971; *Suaeda monoica*) due partly to the low permeability of Na^+ to the tonoplast. That the tonoplast may act as a strong barrier against the movement of Na^+ than that of K^+ to the vacuoles has already been demonstrated (*Sauaeda maritima*: Yeo, 1974; Cereals: Jeshke, 1979). That a low Na^+/K^+ ratio might result from a high retention of K^+ in the leaf cells is probably a general feature of the *Gramineae* (Albert and Kinzel, 1973) and has also been observed in *Avicennia*, a salt secreting plant (Rains and Epstein, 1967).

On the contrary, where high Na^+ and Cl^- in the excretion was ascribed to active extrusion, the suggestion has been based on measurements of electro-chemical potentials (e.g., *Atriplex*:). While a direct evidence showing extrusion in 'Kallar' grass to be an active process, has not yet been brought forth by any worker so far (e.g., Sandhu et al., 1981; Joshi et al., 1983), the present, and the other studies in our laboratories (Bhatti et al., 1985) showed a close resemblance of the rupture of salt 'glands' of 'Kallar' grass with the development of toxicity symptoms in avocado (Cl^-; Bingham et al., 1968) and wheat (P; Bhatti and Loneragan, 1970). In wheat and avocado leaves, the necrotic symptoms appeared as a result of high concentration of P and Cl^- in the cell walls. According to Oertli's hypothesis"high ion concentrations in cell walls of leaves would affect the water relations of the individual cells but not the transpiration flow from the Xylem through the cell walls. Consequently an increase in the π wall will reduce turgor and/or cell volume (assuming that there are no changes in rates of transpiration and in resistances between leaves and the external solution".

The present data call, therefore, for more elaborate studies involving compartmental analysis of Na^+ and Cl^- in the tissue of leaf blade and those of the salt glands to understand the distribution of Na^+ and Cl^- at the cellular level.

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APPENDIX I

Effect of Phenylmercuric acetate (PMA) on fresh weights of excised leaves of field (Bio-Saline Research Sub-Station, Lahore) sample of 'Kallar' grass at various times after treatment.

(24 hours after treatment)

Time (minutes)	-PMA	+PMA
	Fresh weights (g)	
0	1.0125	0.8123
2	0.9309	0.8075
4	0.9284	0.8035
6	0.9171	0.7984
8	0.9107	0.7943
10	0.9049	0.7899

Rate of transpiration	-PMA	+PMA
$\mu\ell$/min/g	3.66	2.76