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Calcium Chloride and Salinity Stress Effects on Growth, Dry Matter Allocation and Ion Uptake of Sweet Potato (*Ipomoea batatas* [L.] Lam.)

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Abstract

The effects of NaCl salinity and $CaCl_2$ concentrations on growth, dry matter allocation and ion uptake of sweet potato (*Ipomoea batatas* [L.] Lam.) plants were examined. Responses of sweet potato to salinity showed that plants growing in low Ca^{2+} exhibited severe growth reduction under salinity stress of 140 mM NaCl. Growth was reduced by NaCl salinity, and differences in ion uptake were observed between the plants receiving low and high concentrations of $CaCl_2$. Relative growth rate (RGR) of sweet potato was only slightly reduced by salinity in the early stages, with a large reduction occurring in the later stages. Sweet potato had a higher dry matter allocation to its shoots as NaCl salinity reduced root growth more than it did shoot growth. Salinity tolerance of sweet potato appears to be associated with its ability to control rates of Na^+, K^+ and Ca^{2+} ion uptake and transport, in order to maintain ionic adjustments within the plant tissues during salt stress. There appears to be a salt tolerance mechanism operating in which, during salt stress, ionic adjustment within the plant tissues of sweet potato cultivar is maintained by controlling the rates of ion uptake and transport.

Key words: *Ipomoea batatas*, sweet potato, salinity, calcium chloride, Ca, K, Na, relative growth rate, dry matter accumulation, ion uptake

Introduction

Salinity inhibits plant growth and interferes with uptake and transport of essential nutrients (Greenway and Munns, 1980), while calcium is important for proper root development and for maintaining a balanced nutrient ion uptake (Mengel and Kirkby, 1987). Plants unable to cope with high concentrations of ions in the external medium can do little to modify their ion content. They may, however, transfer ions to the shoot, re-export them to the medium through their roots, or redistribute them to various organs and cell components (Hellebust, 1976). The ability to transport Ca^{2+} to the shoot during salt stress is considered by LaHaye and Epstein (1971) to be an indication of salt tolerance.

It has been demonstrated that increasing levels of Ca^{2+} in the external medium alleviates the adverse effects of NaCl salinity on plant growth. Under NaCl stress, the growth of potato was greatly improved by the addition of Ca^{2+} (Bilski et al., 1988). Hyder and Greenway (1965), in an earlier study, found that Ca^{2+} modified the response of *Hordeum vulgare* plants to NaCl salinity. However, NaCl reduced growth of plants much more at low Ca^{2+} than at high Ca^{2+}. LaHaye and Epstein (1971) reported that Ca^{2+} added to the nutrient solution modified the effects of NaCl salinity on bean plants. Cramer et al. (1986) observed that Ca^{2+} partly restored ionic balance and growth to salt stressed cotton plants. They also speculated that high Ca^{2+} protected the cell

membranes from the negative effects of salinity. In their evaluation of two wheat species differing in salinity tolerance, Davenport et al. (1997) found that tolerant wheat was more efficient in utilising Ca^{2+} to inhibit Na uptake than the salt-sensitive species.

In moderate concentrations, Ca^{2+} increased the rates of ion accumulation within the roots and improved the uptake of K^+ under NaCl salinity in cotton (Cramer et al., 1987). Also in cotton plants, Ca^{2+} was found to exert its greatest influence on the selectivity of K^+ over Na^+ at the primary root tip (Zhong and Lauchli, 1994). According to Epstein (1962), this high selectivity of K^+ in the presence of Na^+, in the uptake and transport processes, is largely due to the presence of Ca^{2+} ions in the external solution. In an earlier study, Epstein (1961) demonstrated that Ca^{2+} played a role in selective cation transport by plant cells. Excessive amounts of Na^+ can result in reduced uptake of K^+ and Ca^{2+}, which are both required for maintaining cellular selectivity and integrity. Wyn Jones and Lunt (1967) have indicated the need of Ca^{2+} for the selective transport of K^+ across cellular membranes. According to Lynch et al. (1987), Na^+ ions compete with Ca^{2+} for uptake and affect cellular levels of Ca^{2+}, resulting in cell leakage of ions and loss of membrane integrity. By increasing the level of Ca^{2+} in the saline solution, the competition between Ca^{2+} and Na^+ ions was reduced and cell membrane integrity was restored (Cramer and Lauchli, 1986). Cramer et al. (1987) showed that an adequate supply of Ca^{2+} could greatly reduce or prevent the uptake of Na^+ into roots of salt stressed cotton seedlings and its transport from roots to shoots.

Low concentrations of Ca^{2+} are used in plant cells for cell signaling and are conducted by several different types of Ca^{2+} channels, regulated by different mechanisms (Schroeder and Thuleau, 1991). Plasma membrane Ca^{2+} channels allow the influx of Ca^{2+} from the cell wall, while Ca^{2+} release channels, found within intracellular organelles, release stored Ca^{2+} into the cytoplasm. The influx of Ca^{2+} across the plasma membrane plays a major role in Ca^{2+} signalling, though the role the plasma membrane plays in maintaining adequate levels of cytoplasmic Ca^{2+} during inactive periods is not clearly defined (Bush, 1995). Under salinity stress conditions, an early response to Na^+ stress signals appears to be a rapid increase in free cytosolic Ca^{2+} in plants (Bush, 1995; Knight et al., 1997; Kiegle et al., 2000; Sanders et al., 2002; Donaldson et al., 2004). Bressan et al. (1998) proposed a model for salt stress signalling that allows plants to sense the presence of excess Na^+ and adjust to it by initiating a Ca^{2+}-dependent response to the salinity condition. Furthermore, researchers have identified a genetic locus containing a mutant calcium-binding protein, SOS3, with hypersensitivity to NaCl (Zhu et al., 1998; Halfter et al., 2000; Shabala et al., 2005). Increased levels of Ca^{2+} nullified this hypersensitivity and expression of this trait was suppressed by millimolar levels of Ca^{2+} (Zhu et al., 1998). Available literature indicates that in-depth studies on salinity stress in sweet potato are limited.

The objective of the study was to investigate the effects of NaCl salinity and $CaCl_2$ concentrations on growth and uptake and distribution of Na^+, K^+ and Ca^{2+} in sweet potato. An examination of the effects of inorganic solutes on Na^+ uptake might provide information on the ability of this plant species to tolerate high NaCl stress conditions.

Materials and Methods

Plant material and experimental design

A hydroponic system was set up in the glasshouse of the Plant Science Laboratories at The University of Reading, United Kingdom, using the sweet potato cultivar 'Salyboro'. It consisted of an air pump attached to a mainline of PVC tubing branching alternately at 0.2 m intervals. Each branch was 1.0 m in length, with an aerator attached to the exposed end. The 1.0 m branches were immersed in 5 l plastic buckets containing the plants supported in nutrient solution on polystyrene discs. The polystyrene discs were 21.5 cm in diameter and 3.0 cm thick. Four equally spaced holes of 2.5 cm diameter were cut into the polystyrene discs. Plants were supported within the holes in the discs with 1.5 cm thick sponge bungs. The buckets were wrapped in aluminium foil to reduce lighting, in an effort to minimise growth of algae within the nutrient medium.

The composition of the nutrient solution (Wheeler et al., 1990), excluding the Ca element, were as follows: NH_4NO_3 (7.5 mmol l^{-1}), KH_2PO_4 (0.5 mmol l^{-1}), KNO_3 (3.0 mmol l^{-1}), $Mg(NO_3)_2.6H_2O$ (1.0 mmol l^{-1}), Fe(EDTA)Na (60.0 mmol l^{-1}), H_3BO_3 (19.0 mmol l^{-1}), $MnSO_4.4H_2O$ (3.7 mmol l^{-1}), $ZnSO_4.7H_2O$ (0.32 mmol

l^{-1}), $CuSO_4.5H_2O$ (0.13 mmol l^{-1}), and Na_2MoO_4 (0.04 mmol l^{-1}).

Forty-day-old sweet potato plantlets were hardened off for two weeks and then transferred to the polystyrene discs supported in the plastic buckets filled with a nutrient solution. The nutrient solutions were continuously aerated and renewed every seven days. Glasshouse temperature was maintained at approximately 20°C. Supplementary lighting was provided to maintain a photoperiod of 16 h per day. The sweet potato experiment was arranged in a completely randomised design. Treatments consisted of all possible four $CaCl_2$/NaCl combinations: 2.99 mM $CaCl_2$ without NaCl (control), 15.0 mM $CaCl_2$ without NaCl (control), 2.99 mM $CaCl_2$ with 140 mM NaCl, or 15.0 mM $CaCl_2$ with 140 mM NaCl. Each $CaCl_2$/NaCl combination was replicated four times and for each destructive harvest, four plants were sampled for each treatment. Plants were harvested destructively on days 0, 7, 14, 21 and 28 after exposure to the salt treatments.

Growth measurements

At each destructive harvest, the material was examined for the following characteristics: plant height, number of shoots, number of nodes, number of fully expanded leaves, shoot fresh weight, root fresh weight, number of roots, shoot height, number of shoots, number of nodes, shoot dry weight, root dry weight, Na^+, K^+, Ca^{2+} content of leaves and Na^+, K^+, Ca^{2+} content of roots.

Na^+, K^+ and Ca^{2+}determination

Solute concentrations of plant tissues were determined according to the standard procedures of the Biochemistry Unit of the School of Plant Sciences Laboratories, The University of Reading. Leaf, stem and root tissues were analysed for Na^+, K^+ and Ca^{2+} contents. Plant material was prepared for drying by lightly rinsing to remove surface salts from roots, divided into shoots and roots, and then weighed. After drying and weighing of the plant material resulting from the experiment, four 0.5 g leaf and root samples from each treatment were weighed in a 50 ml beaker, to which was added 5 ml of concentrated nitric acid. This procedure was done under a fume cabinet. Initial digestion of the material took about 5 minutes before placing the beaker on a hot plate. After digestion of the material for about 5-10 minutes, a further 10-15 minutes was required to boil off the acid until about 1 ml was left in the beaker. After cooling the contents, a small volume of distilled H_2O was added to each beaker, and the contents filtered. Each sample was then made up to a volume of 25 ml with distilled H_2O. The Na^+, K^+ and Ca^{2+} contents were then determined by flame photometry.

Calculations

Root to shoot ratio:

Root-shoot ratio is the ratio of root dry weight to shoot dry weight

Relative growth rate, Net ion uptake and transport:

Relative growth rate (RGR) was calculated using the formula:

$$RGR = (\log_e W_2 - \log_e W_1)/ (T_2 - T_1),$$

where W_1 and W_2 were weights of plant parts at harvest times T_1 and T_2.

The rates of net ion uptake (J) and transport (J_s) were calculated as:

$$J = (Q_2 - Q_1)/WR\ (T_2 - T_1),$$

$$J_s = (Qs_2 - Qs_1)/WR\ (T_2 - T_1),$$

where Q_1 and Q_2 were ion contents of the whole plants; Qs_1 and Qs_2 were ion contents of the shoot at harvest times T_1 and T_2; WR was the average root weight between times T_1 and T_2, i.e.

$$WR = (WR_2 - WR_1)/\log_e(WR_2/WR_1),$$

where WR_1 and WR_2 were root fresh weights at harvest times T_1 and T_2.

Net uptake by root $= J - J_s$

(above calculations taken from Storey, 1995)

Statistical analyses

Analysis of variance (ANOVA) was conducted on all experimental results using SAS's analytic procedures (SAS Institute, Cary, NC, USA).

Results and Discussion

After 28 days of exposure to varying NaCl and $CaCl_2$ concentrations, treatment differences were apparent in the response of the sweet potato cultivar 'Salyboro'. Visual symptoms on NaCl-stressed plants included the shedding of leaves and necrotic lesions in the roots.

Analyses of variance of the growth responses (Table 1) showed that the growth interval (time) had a highly significant effect on shoot fresh and dry weights, number of roots and total dry weights. Only a few of these characters were affected by NaCl salinity. There were also significant interactions, most notably NaCl salinity with $CaCl_2$ concentration, which affected several of the growth responses.

Root dry matter production was reduced in the presence of 140 mM NaCl (Fig. 1), although analysis of variance results (Table 1) did not indicate significance. When 15 mM $CaCl_2$ was added to the nutrient solution, there was some improvement on the adverse effects of NaCl on leaf and root dry matter production. Root dry matter production decreased for all treatments, with the exception of the NaCl-stressed plants exposed to low $CaCl_2$. Root growth in this case was stimulated by the stress conditions.

The NaCl-treated plants produced less total dry matter at the end of the experimental period than did their corresponding unstressed high and low $CaCl_2$ treated plants. These effects are seen in Fig. 1. While there was a slight reduction in shoot RGR with the addition of 140 mM NaCl to the nutrient solution (Table 2), a more drastic reduction was seen in root RGR for this level of salinity. A higher level of $CaCl_2$, had a negative effect on shoot growth, whereas root growth was greatly enhanced by the addition of 15 mM $CaCl_2$ to the nutrient solution, for both stressed and unstressed 'Salyboro' roots.

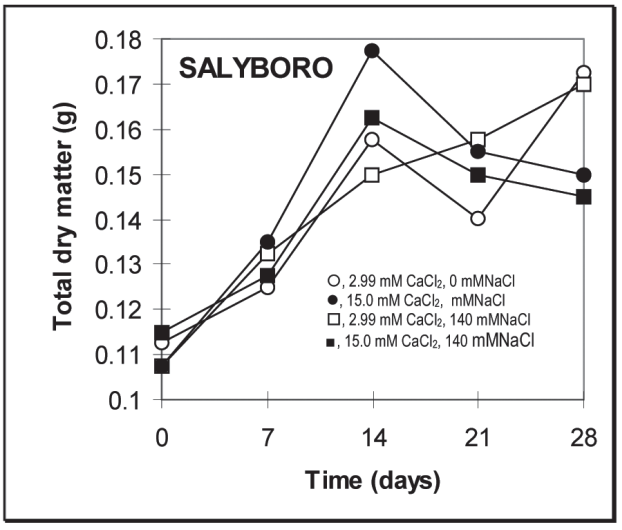

Fig. 1. Effect of salinity and low and high $CaCl_2$ concentrations on the total dry matter production of the sweet potato cultivar 'Salyboro' over time

Shoot growth was significantly reduced in the presence of 140 mM NaCl in the growth medium, which suggests *I. batatas* to be a moderately salt sensitive plant species. The adverse effects of salinity were also seen in the shoot by a reduction in the number of leaves, shoot height and number of nodes. In two separate studies, Benzioni et al. (1992) found that the number of nodal segments produced by *in vivo* grown whole plants of the salt tolerant jojoba (*Simmondsia chinensis*) were reduced by increasing NaCl levels, and when compared with *in vitro* grown nodal segments (Mills and Benzioni, 1992), the whole plants responded to salinity in a similar

Table 1. Analysis of variance of selected growth responses of the sweet potato cultivar 'Salyboro' under increasing NaCl and $CaCl_2$ concentrations

		Significance levels							
Source	df	Plant height (cm)	Shoot fresh weight(g)	Shoot dry weight(g)	Number of roots	Root length (cm)	Root fresh weight (g)	Root dry weight(g)	Total dry weight (g)
Time	4	**	***	***	***	**	NS	*	***
Salinity	1	NS	***	NS	NS	**	NS	NS	NS
Calcium	1	NS	NS	NS	NS	NS	NS	NS	NS
Sal x Cal	1	*	*	NS	NS	*	**	NS	NS
Sal x Time	4	NS	***	NS	***	NS	NS	NS	NS
Cal x Time	4	NS	NS	NS	NS	**	NS	NS	NS
Sal x Cal x T	4	NS	NS	NS	NS	NS	**	NS	NS
Std Err		0.65	0.07	0.009	0.80	1.41	0.03	0.003	0.01

Error mean square has 60 df. *, ** and *** denote statistical significance at 5, 1 and 0.1% level of confidence, respectively. NS indicates differences between means not significant.

Table 2. Relative growth rates of shoot, root and whole plant and shoot to root ratios of the cultivar 'Salyboro' treated with $CaCl_2$ and two NaCl concentrations for 28 days

Treatment Ca/Na (mM)	Relative growth rates (g g^{-1} dry wt day^{-1}) Shoots	Roots	Whole plant	Shoot : root ratio
2.99/0	0.018±0.005	0.015±0.006	0.017±0.005	3.55±1.6
2.99/140	0.017±0.007	0.003±0.008	0.014±0.005	1.70±1.7
15.0/0	0.015±0.007	0.028±0.011	0.016±0.007	2.75±0.2
15.0/140	0.010±0.007	0.021±0.011	0.011±0.004	1.20±0.1

(mean ± SE, $n = 4$)

manner. Potluri and Prasad (1993) also reported a decrease in shoot height and number of nodes with increasing salt concentration in *in vitro* grown potato cultivars exposed to NaCl concentrations ranging from 0.2 - 1.0%. Lower salt concentrations (0.2% NaCl) increased shoot height in most of the cultivars under study, and while it was greatly reduced at concentrations higher than 0.2% NaCl, plants were able to sustain relatively high dry weights. This, according to the researchers, was due to the accumulation of both organic and inorganic ions.

It is evident from the data presented here that by increasing the $CaCl_2$ supply to the nutrient solution, the harmful effects of NaCl on growth of the sweet potato are moderated. When the $CaCl_2$ content of the nutrient solution was 2.99 mM, Ca^{2+} deficiency symptoms were observed in both roots and shoots of the salt stressed sweet potato cultivar 'Salyboro'. These symptoms were similar to those observed in Ca^{2+} deficient salt stressed corn reported by Maas and Grieve (1987). An increase of 15.0 mM $CaCl_2$ in the nutrient solution alleviated the deficiency symptoms. Growth of the sweet potato plants was reduced by NaCl salinity; NaCl-induced changes in growth and ionic concentrations of plants have been reported by Cachorro et al. (1993), who concluded that growth inhibition by the salt sensitive *Phaseolus vulgaris* could be due to the toxic effects of ions which this plant species may not be able to partition effectively.

The responses of relative growth rate (RGR) of the sweet potato appeared to be slightly reduced by salinity during the earlier stages, with a larger reduction occurring in the later stages of growth. The decrease in RGR as a result of NaCl salinity was higher in the low $CaCl_2$ treatments, indicating the existence of an effect of salinity and $CaCl_2$ concentration on growth. Other studies (Akita and Cabuslay, 1990; He and Cramer, 1993) have also reported a salinity-induced reduction in RGR. There was a higher dry matter allocation to the sweet potato shoots than to its roots, as NaCl salinity reduced root growth more than it did shoot growth. This supports Romero and Marañón (1996) who found that under salt stress, annual sweet clover (*Melilotus segetalis*) allocated more biomass to leaves, rather than to roots.

The solute contents of leaf and root tissue were analysed (Table 3) and most of them showed significance for stage of growth (time). Sodium concentrations increased over time for the NaCl-stressed plants. There was also a highly significant effect of Ca^{2+} on leaf Na^+ content. Significant differences were found only for NaCl salinity on leaf solute concentrations of Ca^{2+}. The concentrations of Na^+, K^+ and Ca^{2+} in the leaf and root tissue of sweet potato cultivar 'Salyboro' are presented in Fig. 2.

The concentrations of Na^+, K^+ and Ca^{2+} in the leaf and root tissue of sweet potato cultivar 'Salyboro' are presented in Fig. 2. Sodium concentrations in the leaf tissue of NaCl-stressed plants subjected to both low and high $CaCl_2$ were constant between 0 and 7 days, and then increased steadily from day 7 to the end of the 28 day period. Leaf tissue Na^+ concentrations remained fairly constant for unstressed plants. The Na^+ concentrations in the root tissue of stressed and unstressed plants subjected to high $CaCl_2$ followed a similar pattern, fluctuating between 0 and 14 days, and then rising dramatically from day 21 to day 28.

Accumulation patterns of the K^+ ion in leaf tissue (Fig. 2) fluctuated in a very similar manner in all treatments. Leaf tissues experienced a rapid drop in concentration from day 0 to day 7, followed by an increase at day 14 which declined at day 21, then increased again at the end of day 28. Concentrations for each treatment were not significantly different from one another.

Table 3. Analysis of variance of solute accumulation in leaf and root tissue of the sweet potato cultivar 'Salyboro' under increasing NaCl and $CaCl_2$ concentrations

		Significance levels					
Source	df	Leaf Na^+	Leaf K^+	Leaf Ca^{2+}	Root Na^+	Root K^+	Root Ca^{2+}
Time	4	***	***	***	**	*	*
Salinity	1	NS	NS	*	NS	NS	NS
Calcium	1	***	NS	*	NS	NS	***
Sal x Cal	1	NS	NS	NS	NS	NS	NS
Sal x Time	4	NS	*	NS	NS	NS	NS
Cal x Time	4	**	NS	NS	NS	NS	NS
Sal x Cal x T	4	NS	NS	NS	NS	NS	NS
Std Err		67.80	84.56	14.54	294.90	262.81	36.06

Error mean square has 60 df. *, ** and *** denote statistical significance at 5, 1 and 0.1% level of significance, respectively. NS indicates differences between means not significant.

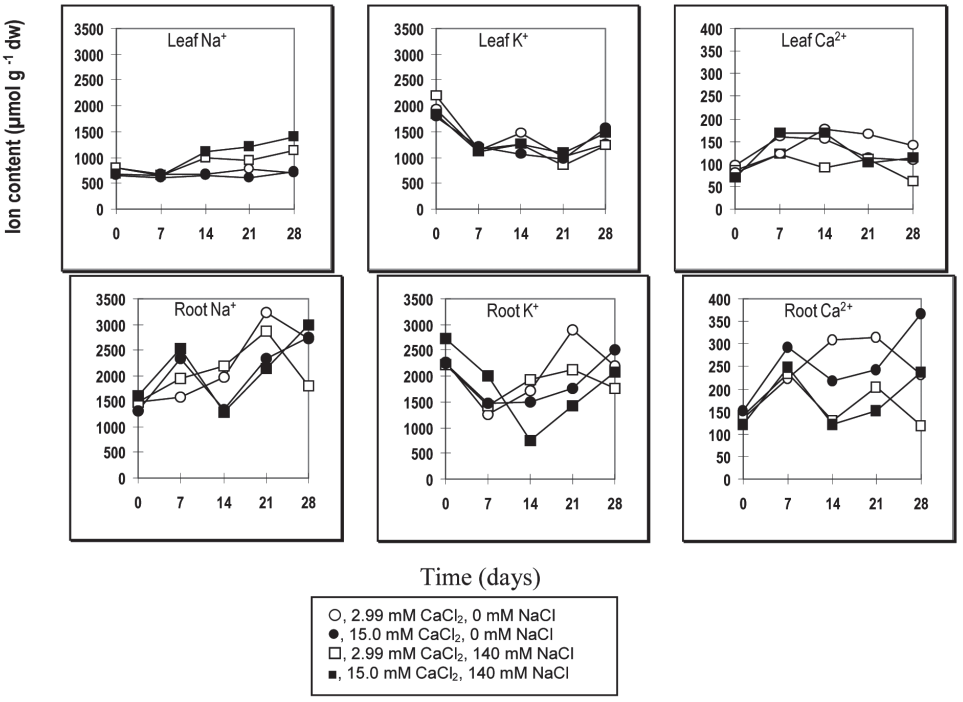

Fig. 2. Effect of salinity and low and high $CaCl_2$ concentrations on the leaf and root mineral composition of sweet potato cultivar 'Salyboro' over time

Weekly measurements of net uptake and transport of Na^+, K^+ and Ca^{2+} ions were taken during the 28 days of the experiment (Table 4). Analysis of variance results (Table 5) showed significant differences over time for net ion uptake of Na^+, K^+ and Ca^{2+} by the whole plant, net ion transport of K^+ and Ca^{2+} from root to shoot and net ion uptake of Na^+, K^+ and Ca^{2+} by the roots.

The pattern of K^+ accumulation followed a similar trend, irrespective of NaCl or $CaCl_2$ treatment. There appeared to be a slow accumulation of K^+ during the first 7 days, followed by a rapid loading of the leaf, stem and root tissues with K^+, with a subsequent decline to lower levels. Root to shoot transport of K^+ ions was equally low. The high uptake of K^+ into the leaf, stem and root during the earlier stages of growth seemed to counteract the negative effects of Na^+ uptake into these plant parts, as total dry matter production was the same for both stressed and unstressed plants. It was only during the later stages of growth that differences in salt treatments became apparent, when stressed plants experienced a decrease in total dry matter production accompanied by a decrease in K^+ accumulation. Asch et al. (1999)

Table 4. Relative growth rate, net ion uptake by whole plant, root to shoot net ion transport and net ion uptake by roots of 'Salyboro' sweet potato

			Net uptake by whole plant (J) (μ mol g^{-1} day^{-1})			Net transport from root to shoot (J_s)(μ mol g^{-1} day^{-1})			Net uptake by root (J - J_s) (μ mol g^{-1} day^{-1})		
Time (days)	Treatment	RGR* ($g\ g^{-1}\ day^{-1}$)	Na^+	K^+	Ca^{2+}	Na^+	K^+	Ca^{2+}	Na^+	K^+	Ca^{2+}
0-7	C_1S_1	0.015	83.76	-1017	67.9	71.78	-632.04	81.18	11.98	-384.95	-13.27
	C_1S_2	0.035	391.25	-1557.37	64.49	94.88	-1163.45	123.14	296.37	-393.92	-58.65
	C_2S_1	0.025	139.5	-1684.09	75.53	73.91	-121.48	36.72	65.59	-1562.61	38.81
	C_2S_2	0.020	443.06	-1049.32	102.5	99.73	-775.71	70.35	343.32	-273.61	32.15
7-14	C_1S_1	0.044	162.68	270.96	25.27	-26.96	125.58	135.64	189.64	145.38	-110.37
	C_1S_2	0.024	188.59	452.42	-97.86	247.76	270.71	107.72	-59.16	181.71	-205.58
	C_2S_1	0.054	-827.65	-150.32	-23.39	-62.17	-132	181.81	-765.49	-18.32	-205.2
	C_2S_2	0.019	-346.5	-575.42	-61.77	116.34	-85.17	131.1	-462.85	-490.25	-192.87
14-21	C_1S_1	-0.010	556.09	174.74	-23.33	149.82	-244.25	100.05	406.28	419	-123.38
	C_1S_2	0.010	569.59	-231.88	76	168.79	-377.27	68.3	400.8	145.39	7.7
	C_2S_1	-0.011	550.13	160.97	30.19	38.4	-24.84	116.13	511.73	185.81	-85.95
	C_2S_2	-0.006	979.03	404.67	-10.1	647.33	120.77	121.64	331.7	283.9	-131.75
21-28	C_1S_1	0.024	-366.44	-237.44	-40.29	-94.32	173.07	96.19	-272.12	-271.75	-136.48
	C_1S_2	-0.001	-325.11	-109.2	-78.42	67.9	137.49	83.38	-393.01	-246.69	-161.8
	C_2S_1	-0.008	331.65	708.39	78.61	140.4	365.61	133.56	191.24	342.77	-54.95
	C_2S_2	0.005	-135.14	25.95	56.08	-371.39	205.58	71.27	236.24	-179.64	-15.19

C_1 = 2.99 mM $CaCl_2$, C_2 = 15.0 mM $CaCl_2$. S_1 = zero NaCl, S_2 = 140 mM NaCl. RGR = relative growth rate, using values for shoot dry weights. Negative values indicate a net loss of the ion from the whole plant or root for the given period

observed a similar effect of K^+ on Na^+ content in rice genotypes affected by salinity. Greenway and Munns (1980) have determined that the K^+ concentrations of various plant species are severely reduced under salinity stress conditions.

The data in Table 6 show the rates of net uptake and transport of the Na^+, K^+ and Ca^{2+} ions, which were calculated for the period from the beginning of the experiment to day 28. Increases in net uptake of Na^+ and by the whole plant were accompanied by decreases in relative growth rate (Table 2). There was a net loss of K^+ ions from the whole plant with decreases in RGR.

The pattern of ion accumulation and the uptake and transport of Na^+, K^+ and Ca^{2+} ions within the sweet potato cultivar were examined. In this experiment, the calculations of uptake and transport of these ions are rather crude measurements based on a simple model by Storey (1995), who related ion transport to levels of ions in the leaves of salt-stressed citrus. Though analyses of variance results showed no significant difference in the effect of salinity on ion concentrations, some variation in Na^+, K^+ and Ca^{2+} contents within the plant tissues were evident. Concentrations of Na^+ depended upon NaCl and $CaCl_2$ concentrations of the nutrient solution. Under NaCl stress, Na^+ concentrations of the roots were higher than other plant parts. In general, leaf concentrations of Na^+ increased with time, while stem and root concentrations declined with time. These observations may indicate a mechanism for accumulating Na^+ within the leaf tissues, and are in agreement with Greenway et al. (1965), Taleisnik (1989) and Romero et al. (1994) who documented

Table 5. Analysis of variance of relative growth rate and rates of ion uptake and transport in the sweet potato cultivar 'Salyboro' under increasing NaCl and $CaCl_2$ concentrations

		Significance levels									
Source	df	Relative growth rate (RGR)	Net Na^+ uptake (J)	Net K^+ uptake (J)	Net Ca^{2+} uptake (J)	Net Na^+ transport (Js)	Net K^+ transport (Js)	Net Ca^{2+} transport (Js)	Net Na^+ uptake by root (J - Js)	Net K^+ uptake by root (J - Js)	Net Ca^{2+} uptake by root (J - Js)
Time	3	NS	***	***	*	NS	***	*	*	***	***
Salinity	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Calcium	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Sal x Cal	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Sal x Time	3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Cal x Time	3	NS	NS	NS	NS	NS	*	NS	*	NS	NS
Sal x Cal x T	3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Std Err		0.02	198.10	209.40	29.99	115.97	120.30	17.64	186.20	168.64	35.07

Error mean square has 48 df. *, ** and *** denote statistical significance at 5, 1 and 0.1% level of significance, respectively. NS indicates differences between means not significant. J = rate of net ion uptake by whole plant, Js = net transport from root to shoot, J - Js = net uptake by root

Table 6. Rates of net Na^+, K^+ and Ca^{2+} uptake and transport of the sweet potato cultivar 'Salyboro' over 28 days of growth in two $CaCl_2$ in the absence of NaCl and at 140 mM NaCl

$CaCl_2$ (mM)	NaCl (mM)	Net uptake by whole plant (J) (μ mol g^{-1} day^{-1})			Net root to shoot transport (J_s) (μ mol g^{-1} day^{-1})		
		Na^+	K^+	Ca^{2+}	Na^+	K^+	Ca^{2+}
2.99	0	110.7	-158.0	12.5	18.5	-137.8	20.3
2.99	140	174.7	-372.9	-13.0	127.6	-317.0	30.4
15.0	0	14.4	-128.7	5.0	48.0	40.6	5.4
15.0	140	295.9	-279.3	17.4	137.7	-210.2	20.2

Negative values indicate a net loss of the ion from the plant

increases in shoot concentration of Na^+ with time in various plant species.

This experiment provides further corroboration of the alleviation of the adverse effects of salinity on *I. batatas* by the addition of Ca^{2+} to the growing medium (Richardson et al., 2003). The salt tolerance of the sweet potato cultivar appears to be associated with its ability to control rates of Na^+, K^+ and Ca^{2+} ion uptake and transport in order to maintain ionic adjustments within the plant tissues during salt stress. Greenway and Thomas (1965) suggest a relationship between growth rate and ion concentration, establishing that regulation of ion concentrations occurs during root to shoot transfer. Peacock et al. (1993) attributed growth reduction due to excess salts in the root zone to ionic imbalances within the plant tissues. There appears to be a salt tolerance mechanism operating in which, during salt stress, ionic adjustment within the plant tissues of the sweet potato cultivar is maintained by controlling the rates of ion uptake and transport. This study also demonstrated an influence of relative growth rates of shoots on the Na^+ ion concentrations of the leaf tissues.

References

Akita, S. and Cabuslay, G.S. 1990. Physiological basis of differential response to salinity in rice cultivars. *Plant Soil*, **123** (2): 277-294.

Asch, F., Dingkuhn, M., Wittstock, C. and Doerffling, K. 1999. Sodium and potassium uptake of rice panicles as affected by salinity and season in relation to yield and yield components. *Plant Soil*, **207**: 133-145.

Benzioni, A., Nerd, A., Rosengartner, Y. and Mills, D. 1992. Effect of NaCl salinity on growth and development of Jojoba clones: I. Young plants. *J. Plant Physiol.*, **139** (6): 731-736.

Bilski, J.J., Nelson, D.C. and Conlon R.L. 1988. The response of four potato cultivars to chlorine salinity, sulphate salinity and calcium in pot experiments. *Am. Pot. J.,* **65** (2): 85-90.

Bressan, R.A., Hasegawa, P.M. and Pardo, J.M. 1998. Plants use calcium to resolve salt stress. *Trends Plant Sci.,* **3** (11): 411-412.

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

Cachorro, P., Ortiz, A. and Cerdá A. 1993. Growth water relations and solute composition of implications of *Phaseolus vulgaris* L. under saline conditions. *Plant Sci.*, **95**: 23-29.

Cramer, G.R. and Lauchli, A. 1986. Ion activities in solution in relation to Na^+-Ca^{++} interactions at the plasmalemma. *J. Exp. Bot.*, **37** (3): 321-330.

Cramer, G.R., Lauchli, A. and Epstein, E. 1986. Effects of NaCl and $CaCl_2$ on ion activities in complex nutrient solutions and root growth of cotton. *Plant Physiol.,* **81:** 792-797.

Cramer, G.R., Lynch, J., Lauchli, A. and Epstein, E. 1987. Influx of Na^+, K^+, and Ca^{++} into roots of salt-stressed cotton seedlings. Effects of supplemental Ca^{++}. *Plant Physiol.*, **83**: 510-516.

Davenport, R., Reid, R.J. and Smith, F.A. 1997. Sodium-calcium interactions in two wheat species differing in salinity tolerance. *Physiol. Planta*, **99** (2): 323-327.

Donaldson, L., Ludidi, N., Knight, M.R., Gehring, C. and Denby, K. 2004. Salt and osmotic stress cause rapid increases in *Arabidopsis thaliana* cGMP levels. *FEBS Letter,* 569: 317–320.

Epstein, E. 1961. The essential role of calcium in selective cation transport by plant cells. *Plant Physiol.,* **36**: 437-444.

Epstein, E. 1962. Mutual effects of ions in their absorption by plants. *Agrochimica,* **6**: 293-322.

Greenway, H. and Munns, R. 1980. Mechanisms of salt tolerance in non-halophytes. *Ann. Rev. Plant Physiol.,* **31**: 149-190.

Greenway, H., Gunn, A., Pitman, M.G. and Thomas, D.A. 1965. Plant response to saline substrates VI. Chloride, sodium, and potassium uptake and distribution within the plant during ontogenesis of *Hordeum vulgare. Aust. J. Biol. Sci.,* **18**: 525-540.

Greenway, H. and Thomas, D.A. 1965. Plant response to saline substrates. V. Chloride regulation in the individual organs of *Hordeum vulgare* during sodium chloride treatment. *Aust. J. Biol. Sci.,* **18**: 505-524

Halfter, U., Ishitani, M. and Zhu, J.K. 2000. The Arabidopsis SOS2 protein kinase physically interacts with and is activated by the calcium-binding protein SOS3. *Proc. Nat. Acad. Sci.,* USA **97**: 3735–3740.

He, T. and Cramer, G.R. 1993. Growth and ion accumulation of two rapid-cycling Brassica species differing in salt tolerance. *Plant Soil,* **153**: 19-31.

Hellebust, J.A. 1976. Osmoregulation. *Ann. Rev. Plant Physiol.*, **27**: 485-505.

Hyder, S.Z. and Greenway, H. 1965. Effects of Ca^{++} on plant sensitivity to high NaCl concentrations. *Plant Soil,* **23**:258-260.

LaHaye, P.A. and Epstein, E. 1971. Calcium and salt toleration by bean plants. *Physiol. Plant.*, **25**: 213-218.

Kiegle, E., Moore, C.A., Haseloff, J., Tester, M.A., and Knight, M.R. 2000. Cell-type-specific calcium responses to drought, salt and cold in the *Arabidopsis* root. *Plant J.,* **23**: 267–278.

Knight, H., Trewavas, A.J., and Knight, M.R. 1997. Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity. *Plant J.,* **12**: 1067–1078.

Lynch, J., Cramer, G.R. and Lauchli, A. 1987. Salt stress disturbs the calcium nutrition of barley (*Hordeum vulgare* L.). *New Phytol.,* **99**: 345-354.

Maas, E.V. and Grieve, C.M. 1987. Sodium-induced calcium deficiency in salt-stressed corn. *Plant Cell and Environ.,* **10**: 559-564.

Mengel, K. and Kirkby, E.A. 1987. *Principles of Plant Nutrition.* International Potash Institute, Bern, Switzerland.

Mills, D. and Benzioni, A. 1992. Effect of NaCl salinity on growth and development of Jojoba clones: II. Nodal segments grown *in vitro. J. Plant Physiol.*, **139** (6): 737-741.

Peacock, C.H., Dudeck, A.E. and Wildmon, J.C. 1993. Growth and mineral content of St. Augustinegrass cultivars in response to salinity. *Hort. Sci.*, **118** (4): 464-469.

Potluri, S.D.P. and Prasad, P.V.D. 1993. Influence of salinity on auxiliary bud cultures of six lowland tropical varieties of potato (*Solanum tuberosum*). *Plant Cell Tissue Organ Cult.,* **32** (2): 185-191.

Richardson, K.V.A., Caligari, P.D.S. and Wetten A.C. 2003. Cell and nuclear degradation in sweet potato (*Ipomoea batatas* [L.] Lam.) root meristems following exposure to salinity. *Trop. Agric. (Trinidad),* **80** (4): 227-234.

Romero, J.M. and Marañón, T. 1996. Allocation of biomass and mineral elements in *Melilotus segetalis* (annual sweet clover): effects of NaCl salinity and plant age. *New Phytol.*, **132** (4): 565-573.

Romero, J.M., Marañón, T. and Murillo, J.M. 1994. Long-term responses of *Melilotus segetalis* to salinity. II. Nutrient absorption and utilisation. *Plant Cell Environ.,* **17**: 1249-1255.

Sanders D., Pelloux, J., Brownlee, C., and Harper, J. F. 2002. Calcium at the crossroads of signaling. *Plant Cell,* **14** (Suppl S), S401–S417.

Schroeder, J.I. and Thuleau, P. 1991. Ca^{2+} channels in higher plant cells. *Plant Cell,* **3**: 555-559.

Shabala, L., Cuin, T. A., Newman, I. A. and Shabala, S. 2005. Salinity-induced ion flux patterns from the excised roots of Arabidopsis *sos* mutants. *Planta,* **222**: 1041–1050.

Storey, R. 1995. Salt tolerance, ion relations and the effect of root medium on the response of citrus to salinity. *Aust. J. Plant Physiol.*, **22**: 101-114.

Taleisnik, E.L. 1989. Sodium accumulation in *Pappophorum.* I. Uptake, transport and recirculation. *Ann Bot.,* **63** (2): 221-228.

Wheeler, R.M., Mackowiak, C.L., Sager, J.C., Knott, W.M. and Hinkle, C.R. 1990. Potato growth and yield using Nutrient Film Technique (NFT). *Am. Pot. J.,* **67** (3): 177-187.

Wyn Jones, R.G. and Lunt, O.R. 1967. The function of calcium in plants. *Bot. Rev.*, **33**: 407-426.

Zhong, H. and Lauchli, A. 1994. Spatial distribution of solutes, K, Na, Ca and their deposition rates in the growth zone of primary cotton roots: effects of NaCl and $CaCl_2$. *Planta,* **194** (1): 34-41.

Zhu, J.K., Liu, J. and Xiong, L. 1998. Genetic analysis of salt tolerance in Arabidopsis: evidence for a critical role of potassium nutrition. *Plant Cell,* **10:** 1181–1191.