

Effect of sodium chloride and sodium sulphate on growth, water relations and solute adjustment in two sugarcane varieties

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ABSTRACT

Objective of this study was to compare whole plant growth and physiological response to salt stress of two varieties of sugarcane ('CoLk 8102' and 'Co 1148'). Salt stress was induced by adding NaCl, Na₂SO₄ and their combinations. After 100 days of salinization under such stress, the plants of the two varieties responded differently because water potential and osmotic potential decreased with salinity and the lower osmotic potential enabled the plants to maintain turgor. Due to this the water balance was maintained in plant system. Accumulation of ions, such as sodium, potassium and calcium along with proline could explain such osmotic adjustment. 'CoLk 8102' showed higher absorption of potassium than the variety 'Co 1148' which had conferred tolerance to 'CoLk 8102'.

Key words: Salinity, Sugarcane, Osmotic potential, Dissolve salts, Osmolytes

As a C₄ plant, sugarcane has a higher water and temperature optima for growth. According to irrigation schemes, sugarcane needs to be watered at frequent intervals (at 15 days) for optimum growth (Qureshi *et al.* 2002). With irrigation water, in marginally or moderately saline fields, an excess of soluble salts are inevitably taken up, which accumulate in the aerial parts and reduce growth and yield (Akhtar *et al.* 2003). The quality of water is an important consideration for any appraisal of saline or alkaline conditions in an irrigated area. Irrespective of the sources of irrigation water, some salt are dissolve therein. These salts affect the physical and chemical properties of the soil and ultimately the crop growth. The high sucrose and low fiber varieties of sugarcane were adversely affected by salt content (Raheja *et al.* 1962).

Adverse effects of low external water potential can be remedied by uptake of electrolytes but such uptake also creates the toxicity of ions excess (Greenway and Munns 1980) and reported that high ion concentration in cell walls could reduce turgor. Thus, ion regulation and osmo-regulation are subjects of intensive research into possible mechanisms of salt tolerance (Hellebust 1976). K⁺ and Cl⁻ play a key role in salt-tolerance in sugarcane and organic solutes contribute mainly to counteract the negative water potential (Gandonou *et al.* 2006). With osmotic adjustment, some species can maintain a positive turgor potential required for cell enlargement and stomatal opening (Jones and Rawson 1979). Although photosynthetic rate was decreased by salt stress, but in salt tolerant variety it was maintained at a higher level (Yousif *et al.* 2010). Both elastic and osmotic adjustment help to maintain turgor at lower tissue water potential and prevent mechanical damage to plasma membrane (Shihe *et al.* 1994).

The soil solution of saline soils is composed of a range of dissolved salts, such as NaCl, Na₂SO₄, MgSO₄, CaSO₄, MgCl₂, KCl, and Na₂CO₃, each of which contribute to salinity stress (Rengasamy 2002; Munns and Tester 2008). The reductions in growth from high salinity are the consequences of both osmotic stress inducing a water deficit and effects of excess Na⁺ and Cl⁻ ions on critical biochemical processes (Munns and Tester 2008).

Salt affected land on earth comprises 19% out of 2.8 billion ha of arable land (Szabolcs 1989). Injury to leaves due to excess ion-accumulation might be an important factor controlling the active size of the canopy (Francois and Maas 1999). Increased salinity has an inverse relationship with stomatal conductance and net photosynthetic rate (Curtis and Läuchli 1986; Lopez *et al.* 2002), leading to reduced photo-assimilation and dry matter production (Rozeff 1995).

Salt tolerant plants adopt many strategies that range from morpho-anatomical to physiological and biochemical in nature (Zhu 2001). The physiological ones include the exclusion of ions into physiologically less active parts (Schachtman and Munns 1992), better selectivity of K⁺ over Na⁺ (Wilson *et al.* 2000), and synthesis of compatible osmotica for osmo-protection (Sakemoto and Murata 2002). Plant tolerance to salinity may be more related to the Na⁺ and K⁺ ratio in the cell than the absolute Na⁺ concentration (Qian *et al.* 2001). The salinity resistance in maize has been mainly related to greater flux and cytoplasmic K⁺ concentration (Hajibagheri *et al.* 1989). Reduction in water uptake by the root and hampered cell-water relations are both due to the osmotic component of salinity (Wahid *et al.* 1999a). Tolerant plants adjust osmotically by the synthesis of highly water soluble compatible osmotica (e.g. glycinebetaine, free proline and low molecular weight

sugars) and maintain turgor. Among these, free proline ameliorates salt-induced oxidative damage to membranes (Jain *et al.* 2001), and glycinebetaine buffers the cellular redox potential (Hare *et al.* 1998), maintains Na^+ balance between the cytoplasm and the vacuole (Subbarao *et al.* 2001) and protects cytoplasmic membranes during salt stress (Sakamoto and Murata 2002). Likewise, both reducing and non-reducing sugars contribute to turgor maintenance under salt or water stress (Garg *et al.* 2002).

Sugarcane (*Saccharum* spp. hybrids) grown under irrigation, in arid or semiarid regions is frequently subjected to soil salinity which has become an important environmental constraint to its production (Rozeff 1995). The crop is moderately sensitive to salinity with a threshold for yield reduction at 1.7 dS/m (Hunsigi 1993). Sugarcane is considered as a Na^+ -excluder. The accumulation of salt ions and osmolytes could play an important role in osmotic adjustment in sugarcane cells under salt stress (Patade *et al.* 2008). Saline soil or irrigation water have reduced sugarcane stalk and sugar yield (Wiedenfeld and Irvine 2000) by reducing both stalk population and juice quality (Rizk and Normand 1969) and stalk weight (Syed and El-Swaify 1972). Wiegand *et al.* (1996) found that each dS/m increase in root zone salinity decreased stalk population by 0.6 stalk/m² and individual stalk weight by 0.15 kg, resulting in a stalk yield decrease by 13.7 t/ha. Most studies have shown that salinity reduces Pol %, an estimate of sucrose content, and apparent purity (ratio of Pol to Brix where Brix is an estimate of total soluble solids). The deleterious effects of salinity are reported in ratoon cane also (Bernstein *et al.* 1963). Since the overall sugarcane productivity and sucrose recovery is governed by the cumulative yields of plant and successive ratoon crops, salts affect the growth and crop yields adversely implicating not only the farmer's economies adversely but also prove to be a major bottleneck for sucrose recovery. Sugarcane (*Saccharum officinarum* L.) is widely grown in tropical and subtropical areas and is mostly irrigated with subsoil or canal water. It is ranked moderately sensitive to salinity with a threshold value of 1.4 dS m⁻¹ (Maas 1986). Salinity has a greater effect on the gas exchange parameters of sugarcane (Plaut *et al.* 2000). A reduction in the elongation and expansion of sugarcane leaves under salinity has been attributed to a lowered efficiency of growing tissues to utilize sugars for growth (Kumar *et al.* 1994). A majority of plants divert normal metabolic pathways and increasingly synthesize the compatible solutes to mitigate the adverse effects of salinity (Hare *et al.* 1998). This is true for sugarcane too, as the synthesis of compatible solutes, including 3-dimethylsulfoniopropionate and free proline, has been reported in sugarcane leaves under osmotic stress (More *et al.* 1994). However, more work is imperative on this aspect of sugarcane. Sugarcane shows a steep decline in growth and productivity with a progression in root zone salinity although large genotypic differences occur (Akhtar *et al.* 2003). Rozeff (1995) reported a 50% reduction in the sprouting of sugarcane

at 13.3 dS/m while the same reduction of yield occurred at 9.5 dS/m level of salinity. An excess of ions adversely affected the elongation and differentiation of cane stalk internodes and storage of sucrose therein (Akhtar *et al.* 2001). Lingle and Weigand (1997) noticed an increase in the juice osmolality and a decrease in total soluble solids and sucrose per unit increase in salinity. This may be due to a salt-induced stimulation of the sucrolytic activities of acid and neutral invertases (Tazuke and Wada 2002). Furthermore, the older stalk sections had a higher content of juice- Na^+ , little or no change in Cl^- , and lower content of K^+ than the younger ones (Lingle *et al.* 2000).

Reduction in sugarcane growth might either be due to additive or individualistic effects of osmotic and toxic components of salinity. However, which of the two is more causative is not yet clear. It is surmised that both osmotic and toxic components of salinity differently affect the growth and yield of sugarcane at different growth stages. In present study effect of NaCl and Na_2SO_4 (present in irrigation water) on growth, tissue elasticity and solute adjustment were evaluated in two varieties of sugarcane to identify their variability for traits, with the objective of improving crop performance under salinity.

MATERIALS AND METHODS

Experimental Site

The experiment was conducted at the Indian Institute of Sugarcane Research, Lucknow, India, located at 26° 56' N, 80° 52' E, and 111 m above sea level, which falls in the Agro-Ecoregion 4 [Northern Plain and Central Highlands, Hot Semi-arid Eco-region with Alluvial-derived (N8D2) soils] of India (Sehgal *et al.* 1990). The physico chemical characteristics of the soil are given in Table 1. To ensure sufficiency in micronutrients, the soil was also supplemented with micronutrients, the levels at which the micronutrients and NPK amendments were made are in Table 2. And available micronutrients (Fe, Mn, Cu and Zn) in soils, consequent to micronutrients amendments are given in Table 3. Before planting cane in pots, soil in pots were saturated with water

Table1 Physico-chemical characteristics of soil used for pot culture study

Texture	Sandy loam
pH(1:2.5)	6.25
Organic matter %	0.78
Calcium carbonate %	0.75
EC (dS m ⁻¹) water saturation extract	0.33
Exchangeable sodium %	0.75
Exchangeable adsorption ratio	0.35
Saturation %	45
CEC of Soil (meq/100 gm)	10

Values are mean of three replications

Table 2 NPK and micronutrients addition during preparation of soil

Nutrient	Salts	Amount added to soil ($\mu\text{g g}^{-1}$ soil)
N	NH_4NO_3	150 (N)
P	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	80 (P_2O_5)
K	K_2SO_4	80 (K_2O)
B	$\text{Na}_2\text{B}_4\text{O}_7 \cdot 10 \text{H}_2\text{O}$	1 (B)
Cu	$\text{CuSO}_4 \cdot 5 \text{H}_2\text{O}$	5 (Cu)
Mn	$\text{MnSO}_4 \cdot 4 \text{H}_2\text{O}$	10 (Mn)
Zn	$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	5 (Zn)
Mo	$(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$	0.5 (Mo)
Fe	$\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$	5 (Fe)

Table 3 Available micronutrients in soil consequent upon amendments

Micronutrient	Concentration ($\mu\text{g g}^{-1}$ soil)
Iron	17.91
Cu	5.11
Mn	22.52
Zn	4.52

(Table 4a) and left as such for a week to allow free exchange of nutrients added to soil. Samples were taken from this soil for analysis of pH, calcium carbonate, organic matter, electrical conductivity and saturation % (Jackson 1973). Plants were irrigated with saline water under seven treatments prepared by dissolving sodium chloride, sodium sulphate and their combinations in deionised water as given in Table 4b.

Plant material, growth conditions and process of salinisation

The two cultivars of sugarcane ('CoLk 8102' and 'Co 1148') were grown in soil-pot culture. After growth of 60 days, the plants were irrigated with saline water prepared by dissolving the sodium chloride, sodium sulphate and their combinations as, control (only deionised water), NaCl I (34.2 meq/L), NaCl II (205.1 meq/L), NaCl III (341 meq/L), Na_2SO_4 I (53.6 meq/L), Na_2SO_4 II (353.3 meq/L), Na_2SO_4 III (602.8 meq/L), NaCl I + Na_2SO_4 I (34.2 meq/L+53.5 meq/L), and NaCl II + Na_2SO_4 II (205.1 meq/L+353.5 meq/L) (Table 4b). The intensity of photosynthetically active radiation was measured using a Li-Cor quantum sensor meter (Model LI-1000, Li-Cor, Lincoln, NE, USA) and varied from 380 to 410 $\text{mmol m}^{-2} \text{s}^{-1}$. The total salinization period for two cultivars was 100 days. After digestion of plant samples with $\text{HNO}_3:\text{HClO}_4$ (15:1 v/v), the determination of sodium, potassium and calcium was made on flame photometer.

Growth measurement

Before sampling of the plants, different growth attributes (Table 5) which included, height, leaf area, tiller number, cane weight and plastochron were recorded. After keeping the plant material for 48 h at 85°C , dry weight was recorded on 60th (t_1)

Table 4. Initial composition of irrigation water (a) and concentrations of salt dissolve and their osmotic potential (b) used for inducing salinity (ion) stresses

(a) Initial total composition of the irrigation water

Composition	Parts per million
pH	7.3
TDS**	833
Na	124
Ca	47
Mg	46
Cl	225
SO_4	38
CO_3	6
HCO_3	99
NaCl	327

**Total dissolve solids calculated from conductivity

(b) Dissolve salts concentration, electrical conductivity and osmotic potential of irrigation water used

Treatments	Salt Concentration (mg eq L^{-1}) in	EC dS/m	Osmotic potential (bars)
Control	Irrigation water	0.02	-0.04
NaCl I	34.2	4.0	-1.6
NaCl II	205.1	20	-8.8
NaCl III	341.0	33	-14
Na_2SO_4 I	53.5	5.2	-1.6
Na_2SO_4 II	353.5	22	-8.8
Na_2SO_4 III	602.8	36	-14
NaCl I + Na_2SO_4 I	17.4 + 24.8	9	-3.1
NaCl II + Na_2SO_4 II	105.3 + 176.3	24	-17

and 160th (t_2) days of salinization, the relative growth rate (RGR) was estimated as $\text{RGR} = (\ln \text{DW}_2 - \ln \text{DW}_1) / (t_2 - t_1)$, where DW_1 and DW_2 are dry weight, respectively obtained at the beginning (t_1) and at the end (t_2) of the stress episode. The total period of stress was for hundred days.

Water relations

Pre-dawn leaf water potential was measured with a thermocouple psychrometer (Wescor C 52, sample chambers connected to Wescor HR-33 dew-point microvoltmeter, Logan, UT, USA). Osmotic potential was measured on the same sample following freezing and thawing (Wenkert 1980). Turgor pressure was calculated by difference from corrected osmotic and water potential (Fig 1). Leaf water potential was corrected for dilution by apoplastic fraction (Tyree 1976). Relative water content (RWC) was determined (Table 9) by method of Barrs and Weatherley (1962).

Solute measurement and Estimation of chlorophyll content

Free proline content (Table 10) was determined according to Bates *et al.* (1973). Chlorophyll content (Table 6) was

Table 5. Effect of salinity stress on growth characteristics of sugarcane varieties CoLk 8102 and Co 1148 after 100 days of salinization

Treatments	Plastochron (days)		Cane Height (cm)		Green leaf number/plant		Leaf area (cm ²)/plant		Cane dry wt/plant (g)		Tiller/Plant (Nos.)		Internode (8-11) length(cm)	
	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'
Control	9.1	10	150	122	10	8	375	300	890	686	3	2	18	15
NaCl I	10	12	170	115	9	6	300	200	1229	553	3	2.5	18	13
NaCl II	12	15	125	95	6	4	200	150	414	181	1.5	1	18	12
NaCl III	13	16	105	49	3	2	185	140	371	43	1	1	10	11
Na ₂ SO ₄ I	9.1	10	158	98	7	5	275	198	820	391	2.5	3.5	19	9.8
Na ₂ SO ₄ II	13.3	15	80	45	5	3	155	100	121	63	1	1	20	8
Na ₂ SO ₄ III	17.3	20	58	25	4	2	140	65	62	50	1	1	15	9
NaCl I+														
Na ₂ SO ₄ I	10.8	14	149	78	8	6	280	156	962	172	2.5	1.5	19	10
NaCl II+														
Na ₂ SO ₄ II	15	18.3	60	36	4	3	250	120	70	50	1	0	16	7
CD (< 0.5)	1.13	1.04	2.12	2.23	1.12	1.05	3.23	2.45	3.34	4.23	2.13	0.01	2.10	0.50

Table 6 Effect of salinity stress on chlorophyll content of leaf laminae of two sugarcane varieties after 100 days of salinization

Treatments	Chl a (mg/g)		Chl b (mg/g)		Chl a/b		Total chlorophyll (mg/g)	
	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'
Control	3.51	2.02	1.37	0.71	2.56	2.85	4.88	2.73
NaCl I+	3.11	1.71	1.18	0.63	2.62	2.76	4.00	2.34
NaCl II	1.96	0.56	0.73	0.21	2.67	2.6	2.73	0.77
NaCl III	1.33	1.11	0.53	0.42	2.47	2.64	1.86	1.53
Na ₂ SO ₄ I	3.35	1.01	1.28	0.36	2.61	2.76	4.63	1.37
Na ₂ SO ₄ II	2.54	1.9	0.98	0.7	2.58	2.86	3.52	2.6
Na ₂ SO ₄ III	2.17	1.26	0.97	0.44	2.24	2.83	3.14	1.7
NaCl I+							4.39	1.3
Na ₂ SO ₄ I	3.23	0.94	1.16	0.36	2.79	2.37		
NaCl II+							1.8	0.92
Na ₂ SO ₄ II	1.25	0.62	0.55	0.3	2.8	2.01		
CD (< 0.5)	0.04	0.06	0.012	0.03	0.04	0.01	0.12	0.11

Table 7. Effect of salinity stress on Na, K and Ca (%) in leaf laminae of two sugarcane varieties after 100 days of salinization

Treatments	Na ⁺		K ⁺		Na ⁺ /K ⁺		Ca ⁺⁺	
	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'
Control	0.22	0.23	1.09	0.26	0.20	0.88	1.15	0.76
NaCl I	0.35	0.43	0.49	0.37	0.71	1.16	0.76	2.56
NaCl II	2.1	3.6	2.04	1.71	1.03	0.21	3.46	2.05
NaCl III	2.8	4.2	0.64	0.40	3.3	10.50	1.28	3.07
Na ₂ SO ₄ I	0.18	0.43	0.57	0.22	0.32	1.95	1.15	2.69
Na ₂ SO ₄ II	0.43	2.17	1.3	0.25	0.33	8.68	3.2	1.66
Na ₂ SO ₄ III	2.5	2.68	0.18	0.78	1.39		2.18	2.18
NaCl I+ Na ₂ SO ₄ I	0.33	0.48	1.45	0.51	0.22	0.94	2.17	2.75
NaCl II+					1.27	10.6		
Na ₂ SO ₄ II	1.81	5.45	1.43	0.51			2.43	3.32
CD (< 0.5)	0.10	0.02	0.04	0.02	0.03	0.42	0.03	0.05

estimated by using 80% acetone (Arnon 1949). Soil samples were analyzed for pH (1:2.5), electrical conductivity (EC, 1:2), $\text{CaCO}_3\%$, organic matter (OM) % and saturation percent (SP) by methods described by Jackson (1973). Juice analysis was done in expressed juice samples (Table 11) by method described by Mead and Chen (1977).

Data analysis

The means were compared between cultivars and/or saline treatments by LSD (least significant difference) at 0.05 confidence level using student's t-test.

RESULTS AND DISCUSSION

Effect on cane height

The stalk height was reduced at all the three levels (6, 22 and 60%) of sodium chloride in variety 'Co 1148' but at NaCl I it was increased more than control (13.3%) in variety 'CoLk 8102' other wise decreased in other two levels of sodium chloride by 17 and 30% than control. The magnitude of reduction in height was more in variety 'Co 1148' than 'CoLk 8102'. Similarly, the reduction in height was more (20, 63, 80%) due to sodium sulphate treatment at all the three levels in variety 'Co 1148' than control whereas height was increased by 5% due to Na_2SO_4 I in variety 'CoLk 8102' but decreased by 47 and 63% at II and III levels of Na_2SO_4 than control. This is indicating more decline of height in 'Co 1148' than 'CoLk 8102' with Na_2SO_4 . Similarly, reduction in height due to the effect of NaCl I + Na_2SO_4 I was more (36%) in variety 'Co 1148' as compared with 'CoLk 8102' where it was 1% less than control. But the combined effect of NaCl II + Na_2SO_4 II was more effective in reducing of height of the two varieties by 60 and 70% in variety 'CoLk 8102' and 'Co 1148' (Table 5), respectively.

Effect on green leaf numbers

The green leaf number on per stalk was reduced with increasing levels of NaCl, Na_2SO_4 and combined treatment of sodium chloride and sodium sulphate by 10, 40, 70, 30, 50, 60, 20 and 60% in 'CoLk 8102' whereas reduction was by 25, 50, 75, 38, 63, 65, 25 and 63% in 'Co 1148'. In this way magnitude of reduction in numbers of green leaf laminae was more in variety 'Co 1148' than 'CoLk 8102' (Table 5).

Effect on leaf area

Leaf area was reduced due to treatment of NaCl (I, II, III), Na_2SO_4 (I, II, III) and combination of the two salts (NaCl I + Na_2SO_4 I and NaCl II + Na_2SO_4 II) by 20, 47, 51, 27, 59, 63, 25 and 33% in 'CoLk 8102' whereas reduction was by 33, 50, 53, 34, 67, 78, 48 and 60% in variety 'Co 1148' at same levels of salts (Fig 1). In general the sodium sulphate was more effective in reducing stalk height, green leaf number and leaf area as compared with sodium chloride. But in combined treatments the toxicity due to sodium sulphate was reduced (Table 5).

Effect on fresh weight of the cane

In variety 'CoLk 8102', due to treatment of sodium chloride I, the fresh weight of the cane was increased (38%) as compared with control whereas in 'Co 1148', the fresh weight was decreased (19%). Decrease in cane weight was by 53 and 58% in variety CoLk8102 whereas it was decreased by 74 and 94% in variety 'Co 1148' due to NaCl II and NaCl III, respectively (Table 5). Effect of Na_2SO_4 I, Na_2SO_4 II and Na_2SO_4 III also reduced the cane weight by 8, 86 and 93% in variety 'CoLk 8102' but in variety 'Co 1148' this reduction was 43, 91 and 93%, respectively. The two salts in combination (NaCl I + Na_2SO_4 I) increased the cane weight (8%) in variety 'CoLk 8102' but in variety 'Co 1148' the cane weight was decreased (75%) as compared to control. The treatment of NaCl II + Na_2SO_4 II reduced the fresh weight of cane in 'CoLk 8102' and 'Co 1148' by 92 and 93%, respectively (Table 5).

Effect on number of tillers

The number of tillers (Table 5) was increased by 25% in variety 'Co 1148' due to treatment of NaCl I whereas it remained same in variety 'CoLk 8102' at this concentration compared with control. At II and III levels of NaCl the number of tillers was decreased by 50 and 67% in variety 'CoLk 8102' whereas it was decreased by 50 and 50% in 'Co 1148' at these two levels in comparison to control. At NaCl I + Na_2SO_4 I and NaCl II + Na_2SO_4 II treatments the tiller numbers were decreased by 17 and 67% in variety 'CoLk 8102' and 25 and 100% in variety 'Co 1148' compared with control, respectively.

Effect on internodal length

The internodal length (8-11) was decreased by 13, 20, 27, 35, 47, 55, 35 and 51% in variety 'Co 1148' compared with control at NaCl I, NaCl II, NaCl III, Na_2SO_4 I, Na_2SO_4 II, Na_2SO_4 III, NaCl II + Na_2SO_4 I and NaCl II + Na_2SO_4 II treatments respectively. But in variety 'CoLk 8102' the decrease was 0, 0, 44, -6, -11, 17, -6 and 11% at similar treatments compared with control. It is indicating increase in internodal length at Na_2SO_4 I, Na_2SO_4 II and NaCl II + Na_2SO_4 I treatments in variety 'CoLk 8102' (Table 5).

Effect on plastochron

Plastochron (days), required for development of a leaf lamina, was increased by 10, 32, 43, 0, 46, 90, 19 and 65% in variety 'CoLk 8102' whereas it was increased by 20, 50, 60, 0, 50, 100, 40 and 83% with the treatments of NaCl I, NaCl II, NaCl III, Na_2SO_4 I, Na_2SO_4 II, Na_2SO_4 III, NaCl II + Na_2SO_4 I and NaCl II + Na_2SO_4 II, respectively. It is indicating that time required for development of a single leaf was more in variety 'Co 1148' compared with 'CoLk 8102' (Table 5).

Effect on RGR

The calculated RGR values are shown in Table 8. In variety 'CoLk 8102' RGR values increased by 202% with treatment of NaCl I where as it was decreased by 39% in variety 'Co 1148'. Similarly, increase in RGR was recorded (185%) due

Table 8 Effect of salinity stress on relative growth rate (days⁻¹) after 100 days of salinization on two sugarcane varieties

Treatment	RGR (per day)		RGR (% of control)	
	'CoLk 8102'	'Co 1148'	'CoLk 8102'	'Co 1148'
Control	0.041	0.089		
NaCl I+	0.124	0.054	302	61
NaCl II	0.038	0.06	93	67
NaCl III	0.023	0.038	56	43
Na ₂ SO ₄ I	0.041	0.074	100	83
Na ₂ SO ₄ II	0.023	0.068	56	65
Na ₂ SO ₄ III	0.011	0.006	27	7
Na ₂ SO ₄ I	0.117	0.036	285	40
NaCl II+ Na ₂ SO ₄ II	0.029	0.034	71	38
CD (p < 0.5)	0.01	0.02	5.60	3.23

Table 9 Effects of salinity stress on relative water content (%) of leaf lamina of two sugarcane varieties after 100 days of salinization

Treatments	Relative water content (%)	
	'CoLk 8102'	'Co 1148'
Control	96.2	94.5
NaCl I	92.7	89.9
NaCl II	93.8	91.6
NaCl III	71	64
Na ₂ SO ₄ I	80	67.5
Na ₂ SO ₄ II	86	78.4
Na ₂ SO ₄ III	66	60
NaCl I+Na ₂ SO ₄ I	85.6	83.2
NaCl II+Na ₂ SO ₄ II	76	63
CD (p < 0.5)	2.34	2.12

Table 10 Leaf lamina proline (μmolg⁻¹ DW) concentration of two varieties of sugarcane after 100 days of salinization

Treatments	'CoLk 8102'	'Co 1148'
Control	17	20
NaCl I	25	32
NaCl II	27	32
NaCl III	40	52
Na ₂ SO ₄ I	25	28
Na ₂ SO ₄ II	35	42
Na ₂ SO ₄ III	48	58
NaCl I+Na ₂ SO ₄ I	35	52
NaCl II+Na ₂ SO ₄ II	60	75
CD (p < 0.5)	0.34	0.45

to treatment of NaCl I+Na₂SO₄ I in variety 'CoLk 8102' whereas it was decreased by 60% in variety 'Co 1148' compared to control. Decrease in RGR was 7 and 44% in variety 'CoLk 8102' at NaCl II and NaCl III compared with control (Table 8) but in variety 'Co 1148' this was decreased by 33 and 55%. RGR was similar to control with Na₂SO₄ I treatment in variety 'CoLk 8102' but it was decreased in variety 'Co 1148' by 17%. Na₂SO₄ II and Na₂SO₄ III treatments decreased the RGR by 44 and 73% in variety 'CoLk 8102'

whereas it was decreased by 24 and 93% in variety 'Co 1148' compared with control. The treatment of NaCl II+Na₂SO₄ II decreased the RGR by 29 and 62 % in variety 'CoLk 8102' and 'Co 1148' respectively compared to control. It has indicated that RGR decreased as salinity increased in variety 'Co 1148' but in variety 'CoLk 8102', RGR was increased due to NaCl I and combined treatment of NaCl I + Na₂SO₄ I.

Water potential

The water, osmotic and turgor potential were measured with psychrometer (Fig 1). After 100 days of salinization water and leaf water potential increased with NaCl I (-0.05MPa) and NaCl II (-0.068 MPa) treatment as compared with control (-1.0 MPa) but it was decreased more due to NaCl III (-5.0 MPa) in variety 'CoLk 8102'. Similarly in variety 'Co 1148'

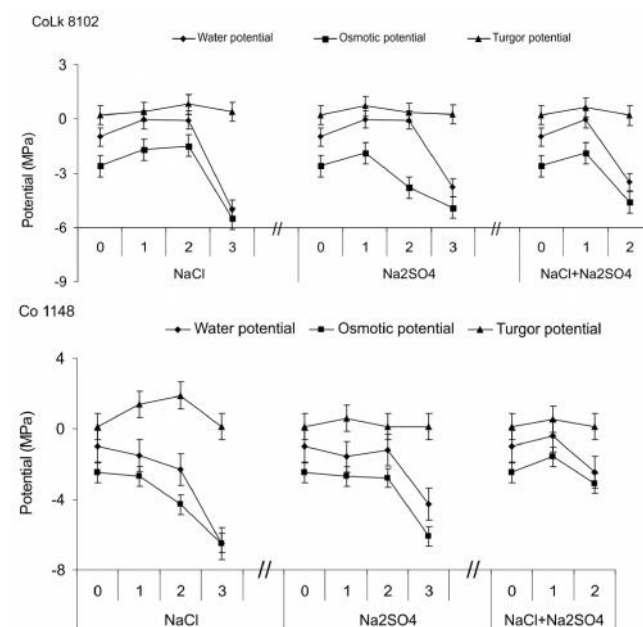


Figure 1 Changes in water, osmotic and turgor potentials after the treatments of different levels NaCl, Na₂SO₄ and their combinations in two varieties of sugarcane. (Values are means ± standard deviation).

Table 11 Effect of different levels of NaCl, Na₂SO₄ and their combinations on juice quality of millable cane after 100 days of salinization on two sugarcane varieties

Treatment	Pol % juice		Purity %	
	'CoLk 8102'	'Co 1148'	'CoLk 8102'	Co 1148'
Control	12.3	12.4	73.7	72.3
NaCl I	10.7	15.8	60.7	92.2
NaCl II	10.5	11.3	69.5	69.8
NaCl III	nil	nil	nil	nil
Na ₂ SO ₄ I	10.0	12.8	68.4	81.6
Na ₂ SO ₄ II	7.8	12.4	52.4	74.3
Na ₂ SO ₄ III	nil	nil	nil	nil
NaCl I+ Na ₂ SO ₄ I	13.7	10.8	77.8	67.6
NaCl II+ Na ₂ SO ₄ II	Nil	Nil	Nil	Nil
CD (p < 0.5)	NS	NS	NS	NS

Table 12 Changes in physico chemical analysis of soil after saline water irrigation after 100 days of sugarcane growth

Treatment	'CoLk 8102'					'Co 1148'				
	pH	EC (dS/m)	CaCO ₃ %	OM %	SP %	pH	EC	CaCO ₃ %	OM %	SP %
Initial value	7.5±0.06	0.18±0.02	0.45±0.03	0.25±0.01	42±0.04	7.5±0.01	0.18±0.01	0.45±0.02	0.25±0.01	42±0.03
Control	7.8±0.03	0.25±0.05	1.1±0.01	0.3±0.02	38±0.03	7.8±0.02	0.27±0.02	1±0.01	0.91±0.03	38±0.01
NaCl I	7.8±0.01	0.2±0.01	0.5±0.02	1.26±0.03	40±0.05	8.7±0.03	0.82±0.04	2±0.03	0.57±0.02	38±0.02
NaCl II	7.8±0.02	1.15±0.23	1.5±0.01	1.6±0.01	38±0.02	8±0.01	7.31±0.52	1.5±0.04	1.56±0.04	38±0.02
Na ₂ SO ₄ I	8±0.03	0.2±0.02	1.7±0.03	1.05±0.04	40±0.06	8.2±0.01	0.82±0.23	1.5±0.05	1.19±0.03	39±0.03
Na ₂ SO ₄ II	8.3±0.01	0.88±0.03	1.2±0.02	0.31±0.01	38±0.05	7.8±0.02	4.89±0.04	1.2±0.03	1.11±0.02	38±0.02
NaCl I + Na ₂ SO ₄ I	8.5±0.01	1.21±0.04	0.5±0.01	1.26±0.03	37±0.03	8.4±0.01	1.21±0.2	2.7±0.02	0.73±0.01	38±0.02
NaCl II+ Na ₂ SO ₄ II	8.8±0.02	18.17±0.03	1±0.01	0.78±0.02	35±0.02	7.7±0.01	14.89±0.01	0.7±0.01	0.37±0.01	38±0.01
CD (p=0.05)	0.32	2.12	0.75	0.32	2.9	0.21	3.21	0.72	0.21	1.2

water potential decreased due to NaCl I (-1.5 MPa), NaCl II (-2.3 MPa) and NaCl III (-6.5 MPa) treatments compared with control (-1.0 MPa). The magnitude of decrease of water potential was more in variety 'Co 1148' as compared to 'CoLk 8102'. The water potential increased with Na₂SO₄ I (-0.04 MPa) and Na₂SO₄ II (-0.069 MPa) treatments as compared with control (-1.0 MPa) but it was decreased more (-3.8 MPa) due to Na₂SO₄ III in variety 'CoLk 8102'. In variety 'Co 1148' water potential decreased due to Na₂SO₄ I (-1.6 MPa), Na₂SO₄ II (-1.2 MPa) and Na₂SO₄ III (-4.3 MPa) compared with control (-1.0 MPa). The water potential was increased due to treatment of NaCl I+ Na₂SO₄ I (-0.04 MPa) but decreased due to treatment of NaCl II+ Na₂SO₄ II (-3.5 MPa) compared with control (-1.0 MPa) in variety 'CoLk 8102' whereas in variety 'Co 1148' decreased due to NaCl I+ Na₂SO₄ I was -0.42 MPa and with NaCl II+ Na₂SO₄ II it was -2.5 MPa compared to control (-1.0 MPa) (Fig 1).

Osmotic Potential

In variety 'CoLk 8102' osmotic potential was increased due to treatment of NaCl I (-1.7 MPa) and NaCl II (-1.5 MPa) but decreased in NaCl III (-5.5 MPa) than control (-2.6 MPa) (Fig 1). In contrast with this in variety 'Co 1148' osmotic

potential was decreased due to these treatments compared with control. The values were -2.7, -4.3 and -6.5 (MPa) due to NaCl I, NaCl II and NaCl III treatments in contrast with control (-2.5). Similarly osmotic potential was increased (-1.9 MPa) in variety 'CoLk 8102' due to treatment of Na₂SO₄ I compared with control (-2.6 MPa) whereas with other treatments like Na₂SO₄ II and Na₂SO₄ III osmotic potential was reduced (-3.8 MPa and -4.9 MPa, respectively). In variety 'Co 1148' this was reduced at all the three levels of Na₂SO₄ (+2.7 MPa, -2.8 MPa and -6.1 MPa) compared with control (-2.5 MPa). The combined treatment (NaCl I+Na₂SO₄ I) increased the osmotic potential in both the varieties (-1.9 and -1.6 MPa) than respective controls (-2.6 MPa and -2.5 MPa) whereas it was decreased (-4.6 MPa and -3.1 MPa) by NaCl II+Na₂SO₄ II treatments in both the varieties than their controls (Fig 1).

Turgor Potential

In variety 'CoLk 8102' turgor potential was increased (100%) due to treatment of NaCl I and NaCl II (300%) but increased only by 100% in NaCl III treatment than control (Fig 1). In contrast with this in variety 'Co 1148' turgor potential was increased by 977% and 1362% due to NaCl I and NaCl II treatments but decreased by 8% with NaCl III

compared with control. Similarly turgor potential was increased (250% more) in variety 'CoLk 8102' due to treatment of Na_2SO_4 I compared with control whereas with other treatments like Na_2SO_4 II and Na_2SO_4 III turgor potential was increased by 75 and 25% more than control, respectively. In variety 'Co 1148' this was increased by 377% with Na_2SO_4 I but it was decreased by 7% and 15% with Na_2SO_4 II and Na_2SO_4 III treatments compared with control. The combined treatment (NaCl I + Na_2SO_4 I) increased the turgor potential in 'CoLk 8102' and 'Co 1148' varieties by 210 and 323% whereas it was decreased by 10 and 8% by NaCl II + Na_2SO_4 II, respectively than respective controls. The maintenance of turgor potential due to these treatments was increased in variety 'CoLk 8102' as compared with 'Co 1148' (Fig 1).

The magnitude of decrease of water and osmotic potential due to Na_2SO_4 I, Na_2SO_4 II and Na_2SO_4 III treatments were approximately same in both the cultivars but loss of turgor potential was more in variety 'Co 1148' than variety 'CoLk 8102' (Fig 1). The combined effect of NaCl I + Na_2SO_4 I decreased the osmotic and water potential with greater magnitude in variety 'CoLk 8102' than 'Co 1148' but maintenance of turgor potential was approximately similar in both the varieties (Fig 1).

Relative water content

With increase in the concentration of NaCl or Na_2SO_4 the value of RWC decreased as compared with control in both the varieties (Table 9) but magnitude of decrease was more in variety 'Co 1148' than 'CoLk 8102'. Due to NaCl treatment decrease in RWC was 4.9, 3.1 and 32.3% in variety 'Co 1148' whereas it was 3.6, 2.5 and 26.2% in variety 'CoLk 8102' with NaCl I, NaCl II and NaCl III treatments, respectively. Due to different levels of Na_2SO_4 the decrease was 28.6, 17 and 36.5% in variety 'Co 1148' but in variety 'CoLk 8102' this decrease was 16.8, 10.6 and 31.4%, respectively with Na_2SO_4 I, Na_2SO_4 II and Na_2SO_4 III treatments. The decrease of RWC was 33.3% in variety 'Co 1148' and 21% in variety 'CoLk 8102' due to combined treatment of NaCl II + Na_2SO_4 II as compared with control but NaCl I + Na_2SO_4 I decreased the RWC by 12 and 11% in 'Co 1148' and 'CoLk 8102', respectively (Table 9).

Ion concentration

Accumulation of sodium ion was more in variety 'Co 1148' compared with 'CoLk 8102' with increase in the levels NaCl and Na_2SO_4 . The accumulation of Na^+ was more in variety 'Co 1148'. The accumulation of K^+ was reverse to the accumulation of Na^+ in both the varieties. In variety 'CoLk 8102' accumulation of K^+ was more and provided tolerance against salinity compared with 'Co 1148' (Table 7). The concentration of Ca^{++} had not changed much either due to NaCl or Na_2SO_4 treatments.

Proline and chlorophyll contents

Both varieties showed increase in proline content with

increase in either NaCl or Na_2SO_4 salts (Table 10). But magnitude of increase was more in variety 'Co 1148' than 'CoLk 8102'. The chlorophyll a and chlorophyll b content decreased with increase in the concentration of NaCl and Na_2SO_4 in both the varieties (Table 6). The combined effect of NaCl II + Na_2SO_4 II reduced the chlorophyll content more as compared with NaCl I + Na_2SO_4 I but decrease in chlorophyll b was more as compared with chlorophyll a. The magnitude of decrease was more in variety 'CoLk 8102' than 'Co 1148' (Table 6).

Physico-chemical changes in soil

The pH (1:2.5), EC (1:2), CaCO_3 (%), organic matter (%) and saturation % of soil was changed due to irrigation of saline water. The major change was observed in electrical conductivity (1:2) of the soil which had increased after 100 days of salinization due to NaCl II + Na_2SO_4 II. The changes of electrical conductivity with other soil characteristics had affected the growth of the cane (Table 12). The saturation % of the soil had decreased due to NaCl and Na_2SO_4 treatments because of decrease in the infiltration of water which resulted into reduced growth of the cane.

Growth and ionic characteristics

Sugarcane varieties indicated significant ($p < 0.01$) differences for the reduction in dry weight, number, leaf area and tillering capacity per plant, with significant ($p < 0.01$) interaction of salinity and varieties. NaCl salinity reduced these parameters in both the varieties but performance of 'CoLk 8102' was better than variety 'Co 1148' (Table 5). Salinity had a more pronounced effect on dry weight than leaf area, which was evident from a significantly ($p < 0.01$) more decrease in specific leaf weight of variety 'Co 1148'.

Both the varieties indicated a significant ($p < 0.01$) difference for the accumulation of leaf Na^+ and Cl^- with increased salinity but K^+ content indicated a concomitant decrease showing a significant ($p < 0.01$) interaction of the varieties with salinity (Table 1). Applied salinity reduced the $\text{K}^+:\text{Na}^+$ ratio, but there was no significant ($p > 0.05$) difference between the varieties. Although Na^+ and Cl^- were detrimental to the growth of varieties, the difference between the varieties was evident. Variety 'CoLk 8102' accumulated markedly lesser Na^+ and more of K^+ than 'Co 1148'. The trend of Na^+ and Cl^- accumulation with growth parameters, however, was negative (Table 5). This carried greater physiological importance in terms of substantial difference between the varieties for the excess of Na^+ on the dry weight, area, and specific weight of leaves. However, a positive correlation of K^+ with these attributes suggested the importance of K^+ to growth in terms of more leaves for the interception of light for photosynthesis as was apparent from the substantially higher leaf dry weight and leaf area of 'CoLk 8102' (Table 5).

Water Relations and osmolytes accumulation

Both varieties differed significantly ($p < 0.05$) in leaf water

status (Figure 2). Although applied salinity reduced water content and water potential of leaves, a significant ($p < 0.01$) difference was discernible between the varieties. 'CoLk 8102' maintained greater relative water content and higher water potential. Although the varieties did not differ ($P > 0.05$) in leaf osmotic potential, 'CoLk 8102' exhibited a steady leaf turgor and better osmotic adjustment. There was a significant ($p < 0.01$) difference in the varieties with regard to accumulation of free proline and soluble sugars. However, an interaction of salinity and varieties was noted for free proline, but not for soluble sugars. Soluble sugars indicated a ~2 fold increase in 'CoLk 8102' at highest salt level over controls (Figure 1), confirming their greater role in the salt tolerance of 'CoLk 8102'. No correlation of soluble sugars appeared with any of the ions. However, free proline accumulated in greater amounts in 'Co 1148' (sensitive variety) and had a positive correlation with Na^+ ($r = -0.769$; $n=8$), suggesting that its accumulation was due to the toxicity of these ions.

Cane yield and juice characteristics

Although 'Co 1148' had a greater stripped cane yield than 'CoLk 8102' under non-saline condition, it suffered a substantial loss due to salinity (Table 11). The most significant ($p < 0.01$) effect of Na Cl was on the quantity of extractable juice. The lowest recovery and most viscous juice occurred at 160 mmol L^{-1} in 'Co 1148', indicating a more reduced water uptake by this variety. This was further evident from the increased juice osmolality having a direct correlation with EC and Na^+ but an inverse correlation with juice- K^+ (Table 11). EC of juice increased with a significant ($p < 0.05$) difference between the varieties. Juice- Na^+ was considerably ($p < 0.01$) greater in 'Co 1148' than 'CoLk 8102', but juice- Cl^- was similar ($p > 0.05$). The K^+ and Na^+ ratio was slightly higher ($p < 0.05$) in the juice of 'CoLk 8102' than 'Co 1148'. Both varieties exhibited differential capability to synthesize total sugars ($p < 0.01$) although salinity had no effect on their accumulation. Contrarily, pol percentage was significantly ($p < 0.01$) higher in the juice of 'CoLk 8102' than 'Co 1148' (Table 11). Correlations between sugar relations and juice ions revealed that increased EC and Na^+ content of juice had a negative relationship with the extractable juice and pol percentage (Table 11). Juice K^+ , on the other hand, indicated a strong positive correlation and apparently a profound effect on the extractable juice and pol percentage of the varieties.

The effect of NaCl I and NaCl I + Na_2SO_4 I was stimulatory in variety 'CoLk 8102' because the value of RGR was 202 and 185% more than control, respectively. Similarly with the treatment of Na_2SO_4 I the RGR was same as it was observed in control (Table 5). But in variety 'Co 1148', the RGR had been less than control in these treatments (Table 1). Similar effect had been observed in weight of cane /plant (Table 5). This clearly depict the salt tolerance was more in variety 'CoLk 8102'. The most obvious morphological difference in salt grown plants, appear from decreased growth, reduction in leaf

area and leaf number (Table 5). The reduced leaf number could be result of excess Na^+ (Table 5) which had induced chlorosis and death of expanded leaf laminae. Such injury are known in many plants (Bernstein 1963) and leads to a decrease in photosynthetic leaf area. As a result and in agreement with finding of Munns and Termaat (1986), the production of carbohydrate declines and productivity fails below a level which could not sustain further growth. Due to reduction in leaf area the cane weight was decreased (Table 5). Further, tiller numbers and internode length were decreased but plastochron duration was increased in variety 'CoLk 8102' due to NaCl III and Na_2SO_4 III treatments. The increase in plastochron duration suggested that leaf development was delayed. The magnitude of decrease was more in variety 'Co 1148'. The combined effect of NaCl II and Na_2SO_4 II treatment decreased the cane weight, tiller number, internode length and increased the plastochron duration in comparison with NaCl I + Na_2SO_4 I treatment (Table 5).

It is evident from leaf water relations that plants had osmotically adjusted to the salt stress imposed on them. Adaptive decrease in plant osmotic potential for maintaining turgor in response to salinity has been widely reported (Bernstein 1963). The maintenance of turgor in salt stressed plants, despite significant growth reduction suggests that turgor was not the main determinant of growth in this study. This implies that factor other than turgor limits the growth. Passioura (1988) postulated that phyto-hormones generated in roots in response to stress reduce growth. Lowering of water potential facilitate continued water uptake from drying soil (Bowman and Roberts 1985). Such a decrease has been reported as a typical result of tissue development under stress and may be related to increased cell wall thickness (Culter *et al.* 1977). The reduced growth (Table 5) observed under NaCl and Na_2SO_4 treatments could be attributed to increasing stiffness of the cell wall probably due to altered structure induced by salinity, as reported by Sweet *et al.* (1990). The other growth parameters which are affected may be due to differences in relative water content also (Joly and Zaerr 1987). The lowering of osmotic potential due to net accumulation of Na^+ , K^+ and proline in leaf laminae, enabled turgor to be maintained at values similar to those of the control (Fig 1). This pattern in mineral composition characterizes these varieties as salt includers. The data show that 'CoLk 8102' had more K^+ in leaves than 'Co 1148'; inducing a lower Na^+/K^+ ratio. This difference may confer a slight advantage on 'CoLk 8102' under salt stress if we accept that K^+ provides better salt tolerance. An increase in proline content has been observed for both varieties (Table 10), could balance low osmotic potential in the vacuolar compartment due to ions (Stewart and Lee 1974).

This study revealed a significant difference between the varieties in terms of reduction in growth and yield characteristics. Better growth and yield of 'CoLk 8102' lied in the higher number and area of leaves together with effective regulation of ions in the leaves. Specific leaf weight, a

determinant of dry matter accumulation (Hunt 1982), was affected more in the 'Co 1148' due to its high sensitivity to Na^+ for dry weight rather than leaf expansion (Plaut *et al.* 2000). Greater reductions in these parameters together with increased signs of salt damage have been regarded as salt sensitivity criteria for many crops (Lutts *et al.* 1996; Wahid *et al.* 1999b; Plaut *et al.* 2000). The symptoms of salt injury were noted to a lesser extent, particularly in the younger leaves of 'CoLk 8102' (data not shown). Enhanced production of supplementary tillers was greatly advantageous to salt tolerant variety in displaying greater photosynthetic area and dry matter yield (Wahid *et al.* 1997; Grattan *et al.* 2002). Changes in ionic status of green leaves are crucial to adjudge the sustenance of the active photosynthetic canopy in giving higher dry matter yield (Francois and Maas 1999). The increased content of Na^+ has been reported to suppress the leaf gas exchange and PSII photochemical activity (Dionisio-Sese and Tobita 2000). In this study, the accumulation of Na^+ and reduction in K^+ took place, but with a substantial difference between the varieties (Table 7). These findings suggest that lowered content of Na^+ in the leaves of 'CoLk 8102' is crucial for better growth and tillering, which was hardly displayed by 'Co 1148'.

Some data are consistent with the idea that high concentrations of proline are essential to tissue with high ion concentration (Greenway and Munns 1980). Nevertheless, proline accumulation does not initiate adoption, but may it be triggered to occur as a result of initiation of other responses to salinity stress (Hasegawa *et al.* 1980). Further despite similar water relations, growth differed under NaCl III and Na_2SO_4 III treatments, suggesting that at high salinity, water relations do not explain differences observed in RGR. Growth reduction observed under high NaCl and Na_2SO_4 conditions could be result of ion excess (Na^+). Differences in K^+ content confer a slight advantage on 'CoLk 8102' under salt stress.

In contrast to some earlier reports (Wilson *et al.* 2000; Qian *et al.* 2001), sugarcane varieties did not show difference in terms of the $\text{K}^+:\text{Na}^+$ ratio (Table 1), thus making it hard to declare it a salt tolerance criterion for this crop. Lingle *et al.* (2000) reported such a trend in the cane stalk stressed with saline irrigation water. This view was further supported by a strong relationship of K^+ , but not of the $\text{K}^+:\text{Na}^+$ ratio, with leaf growth parameters (Table 5). Therefore, absolute rather than relative content of K^+ seems to be a plausible strategy of evaluating salt tolerance in sugarcane as it has crucial roles in osmotic and stomatal regulation and enzymatic reactions (Shrivastava *et al.* 1997; Gratten and Grieve 1999; Dionisio-Sese and Tobita 2000; Lopez *et al.* 2002).

Osmotic adjustment is the improvement in cell water balance due to the accumulation of inorganic and organic osmolytes. Enhanced production and retention of non-toxic compatible osmolytes is a strategy of tolerant plants in countering the damaging effects of salinity. They play numerous roles together with improved cell water balance (cf.

Introduction section). Both the sugarcane varieties indicated remarkable differences for relative leaf water content, leaf water, and turgor potentials, which were substantially greater in 'CoLk 8102' (Figure 1). However, there was no difference in the leaf osmotic potential between the varieties, and the reasons for this are different. The tolerant variety accumulated considerably higher K^+ (Table 7) and had a ~2 fold greater accumulation of soluble sugars (compared to control), but relatively low free proline content at the highest salinity level (Table 10). All these osmolytes improved cell water balance and enabled this variety to adjust osmotically (Figure 1). The sensitive variety, on the other hand, had much reduced water content and very low turgor potential although it also had a higher free proline content. As is revealed from the data, this variety accumulated soluble sugars and K^+ in amounts inappropriate to generate turgor and thus showed reduction in osmotic potential. Free proline accumulation held significant increased as Na^+ was increased (cf. Results section), and its production was more specific to the sensitive variety (Table 7). This suggested that its production was because of salt damage to the cell cytoplasm. This corroborates with what has been reported for soybean (Moftah and Michel 1987), rice (Lin and Kao 1996), sorghum (Wahid *et al.* 1998), and Kentucky bluegrass cultivars (Qian *et al.* 2001). A hampered leaf water status of the 'Co 1148' was further attributed to a reduced water absorption by a weak root system (Wahid *et al.* 1997), followed by its reduced transport to the aerial parts due to the osmotic effect of salinity.

High net leaf carbon assimilation rate followed by rapid translocation of synthesized sucrose to the internodes determines the final yield in sugarcane (Lingle 1999). Applied salinity has a well-pronounced effect on the biosynthesis of sucrose in the leaf and its translocation to stalk for storage (Lingle and Weigand 1997; Akhtar *et al.* 2001). Salinity modulates the activities of sugar metabolizing enzymes in a number of crops. It reduced activities of sucrose synthase and starch phosphorylase and enhanced those of acid and neutral invertases (Krishnamurthy and Bhagwat 1995; Dubey and Singh 1999; Tazuke and Wada 2002). Since phloem loading from source tissue and translocation of photo-assimilates to sink tissue (in addition to other factors) is affected by the sub-optimal availability of water in the medium, the osmotic effect of salinity becomes crucial to this process. This has been evidenced by juice analysis (Table 11). Subsequent to translocation of sugars in the internodes, the excess of ions may stimulate the activity of invertases, which tends to reduce sucrose yield by sucrolytic activity (Balibrea *et al.* 2000; Tazuke and Wada 2002). As noted through juice analysis as NaCl content increased, which had a strong negative trend with extractable juice and brix percentage, as a measure of sucrose concentration (Table 11). It is believed that excess Na^+ in the internodes stimulated the sucrolytic action of invertase, leading to a decreased brix percentage. Although K^+ had a positive correlation with extractable juice and brix

percentage, its effect appeared to be masked by ion-specific action of Na^+ in the internodes.

To conclude, the above-ground growth of sugarcane was largely affected by NaCl -toxicity, and the effect to be that of Na^+ . Soluble sugars and K^+ appeared to lessen the adversaries of ions on tolerant variety by improving the cell water balance to a great extent, while free proline accumulated exclusively as a result of ion-toxicity. At maturity mainly osmotic and, to a lesser extent, toxic effects were evident, the former during the phloem translocation of sucrose and the latter during the sucrolytic action of excess ions on invertases in the internodes. This differential effect i.e. the toxic effect of salinity on leaf growth and osmotic effect on sugar accumulation in stalk may be specific to sugarcane, a fact which should be established in other crops for their better management in saline areas.

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