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Leaf development, transpiration and ion uptake and distribution in sugarcane cultivars grown under salinity

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Abstract

The effects of salinity on leaf growth, initiation and senescence, on transpiration rates, on leaf water potential and on uptake and distribution of several ions were studied in two sugarcane cultivars differing in salinity sensitivity. Plants, growing in a growing mixture in pots, were exposed to salinized irrigation water for 68 days, starting 60 days after planting. EC values of the irrigation water were 1.0, 2.0, 4.0, 8.0 and 12 dS/m, obtained by using a mixture of NaCl and CaCl2. Plants were also grown in nutrient solution and were at a similar age when exposed to a salinity level of 3 dS/m for 30 days followed by 6.0 dS/m for an additional 30 days. Two Na:Ca ratios of 18:1 and 1:2 were used for salinization of the nutrient solution. Both leaf dry weight and area decreased with increasing salinity, but in the more salinity tolerant cultivar H69-8235, the decrease was moderate. Salinity hardly reduced average area per leaf in H69-8235, while the number of leaves declined sharply. This decline was caused by enhanced senescence of mature leaves and not by a decreased rate of leaf initiation. In the more sensitive cultivar, H65-7052, leaf area and initiation of new leaves were sharply reduced by salinity while leaf senescence was less affected. Leaf water potential decreased during the early stages of salinity exposure, and the reduction in water potential was larger in H69-8235. Salinity also decreased the rate of transpiration rate but to a lesser extent than leaf development and growth. The accumulation of Cl and Na in the TVD (top visible dewlap) leaf of the tolerant cultivar H69-8235 was greater than in the sensitive cultivar H65-7052. The concentration of Cl in the TVD leaf was more than 10 times that of Na in both cultivars. The concentration of both ions, but not of K, increased during the early stages of salinity exposure and then remained constant. A gradient in concentration of Cl and Na over the plant was found in both cultivars at all salinity levels, and was steepest between the TVD and younger leaves. No specific Na effect on leaf growth or transpiration could be detected. The accumulation of Cl and Na but not of K occurred primarily in the roots rather than in the leaves and stalks.

Introduction

A considerable amount of information is available regarding the effects of salinity on crop growth and yields, the most evident of which is probably a reductions in growth (Crane and Bowman, 1991; (Greenway and Munns, 1980; Poljakoff-Mayber and Lerner 1993; Yeo et al 1991). This is attributable largely to a decrease in osmotic potential in the root zone, which rapidly affects plant water balance resulting in reduced turgor potential. Plants can respond by adjusting osmotically, thereby partially preventing prolonged loss of turgor. Osmotic adjustment is a result of ion uptake and accumulation and an increase in the concentration of organic solutes. It may also involve changes in tissue water content. (Jacoby, 1993; Munns, 1988; Plaut and Federman 1991). Long-term inhibition of growth under salinity may thus be more a consequence of ion toxicity than of negative water status (Jacoby, 1993; Munns and Termaat, 1986).

Although the rate of canopy development and final size are an outcome of leaf and stem extension-growth, it has been shown that leaf injury and loss due to excess salt ion accumulation might be an important factor controlling the active size of the canopy (Fran-

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cois and Maas, 1993). In addition, the rate at which new leaves are formed determines the total leaf area and therefore the plant's total photosynthetic capacity. It is thus desirable to distinguish between these different components of the overall response of growth to salinity, namely, rates of formation of new leaves, expansion growth, and senescence and injury. Sugarcane is a very appropriate plant for such studies due to the extended period of leaf development and turn over as well as a considerable rate of extension growth.

Salinity may interfere with sugar production in sugarcane in two major manners; by affecting growth and yield and by reducing sucrose concentration in the stalk (Rozeff, 1995). Blackburn (1984) reported that at EC values of saturated pastes (ECe) up to 2–3 dS/m growth and yield of sugarcane was virtually unaffected and that at approximately 7 dS/m a 50% reduction in growth was obtained. Rozeff (1995), similarly, suggested that a steep decline in growth may take place once the ECe rises above 3 dS/m, although plants may survive up to 10–15 dS/m depending on cultivar. Segovia (1989), on the other hand, showed a drastic decrease in growth of sugarcane at fairly low salinity levels.

Differences in salinity tolerance among cultivars of sugarcane have been reported (Bernstein et al., 1966; Dominquez, 1993; Fitch and Moore, 1981; Francois and Maas, 1993; Gomez and Torres, 1993; Meinzer et al., 1994). These differences were mainly in the amount of millable cane produced (Bernstein et al., 1966), biomass production (Dominquez, 1993; Gomez and Torres, 1993), or in tissue sugar concentration (Kumar et al, 1988). Among sugarcane cultivars, greater growth and CO2 assimilation rates under salinity may be associated with initially greater growth and CO2 assimilation rates in unstressed plants of those cultivars regarded as tolerant (Meinzer et al., 1994).

It was suggested that a cellular component of salinity tolerance could be found in cell cultures derived from tolerant and sensitive commercial cultivars (Kresovitch, 1986; Liu, 1986). These findings were, however, never verified. Moreover it is possible that the results were merely due to different potential growth rates of some cultivars in cell cultures (Rozeff, 1995). We thus evaluated differences in salinity tolerance in relation to processes taking place in the whole plant. The objective of the study was to determine the response to salinity of the component growth characteristics responsible for total biomass production in two sugarcane cultivars differing in sensitivity to salinity. The effect of salinity on transpiration rates, and its implications for ion transport, and the specific role of Na as a toxic ion under a wide range of Na:Ca ratios at a constant salinity level were also examined.

Materials and methods

Growing conditions and treatment application

Growing in potting mixture

Two sugarcane (*Saccharum* spp. hybrid) cultivars were grown in a 4:4:1 (v/v/v) mixture of clay soil: commercial potting mixture and volcanic ash in a glasshouse where the day/night temperature regime was typically 35/23°C throughout the experimental period. One cultivar, H69-8235, was considered to be relatively salt tolerant and the second, H65-7052, as relatively sensitive. Stem sections of both cultivars containing two lateral buds were planted in 11-l perforated plastic pots containing this mixture or in vermiculite and were irrigated daily. Fertilizer containing NPK (16-16-16) was first applied to potting mixture-grown plants at 10 days after planting and then every 21 days. Irrigation with salinized water at 5 EC levels consisting of 1 (tap water), 2, 4, 8 and 12 dS $m^{-,1}$ was initiated at 60 days after planting. These irrigation solutions were prepared by dissolving mixtures of NaCl and CaCl2 to give a Na:Ca molar ratio of approximately 4:1. Considering the Ca in the tap water, which was used for irrigation, the SAR was approximately 20. Salinity was gradually raised to reach the predetermined values within 3 days and then continued for 68 days. Irrigation solutions were applied daily in amounts greatly exceeding transpirational losses (150–200%) and the drainage solution was collected quantitatively for analysis.

Growing in nutrient solutions

Stem sections, similar to those planted in the potting mixture were planted in vermiculite and were transferred at the age of 30 days to plastic pots filled with 7-l of aerated, half-strength Hoagland solution (Plaut and Heuer, 1985), one plant per pot. Distilled water was added daily to replace transpirational losses and the solutions were renewed once a week. At 60 days after planting, two solutions of NaCl and CaCl2 mixtures, both at an EC level of 3.0 dS/m but at Na:Ca ratios of 18:1 and 1:2 (approximately SAR values of 40.0 and 4.0) were added each to one-third of the pots, respectively. The remaining one-third of the plants served as controls and were not salinized. Salt concentration was raised in two-thirds of the pots up to

EC of 6.0 dS/m at 90 days after planting with identical Ca:Na ratios and the experiment was terminated at 120 days. Both salinizations were carried out in a stepwise manner during 3 days and the salts were always added in the evening. Nutrient solutions were renewed every 10 days.

Measurements

Leaf formation and senescence were determined by weekly counting of all green leaves (as long as 75% of the leaf was still green, it was considered as a green leaf) and distinguishing between growing leaves above the topvisible dewlap (TVD) leaf and mature leaves from TVD leaf downward. The TVD leaf is the youngest fully expanded leaf. Leaf area was determined from the product of leaf length and leaf width and a factor, which was 0.73. This factor was the slope of the relationship between measured leaf area and the product of leaf length and width (r^2 = 0.936). Leaf water potential was measured with a pressure chamber on segments detached from the TVD leaf (Saliendra et al., 1990). Water potential measurements were always made at midday on clear days.

Transpiration rates of nutrient solution-grown plants were determined once every 7-10 days by weighing of the pots at 1-h intervals between 10:00 and 15:00 h. For the plants grown in potting mixture, transpiration was calculated from the EC of the irrigation and drainage water according to:

$$E = V_i(1 - ECi/EC_d) \quad (1)$$

Where E is the transpiration rate in ml day$^{-,1}$ pot^{-1} V_i, and EC_i are volume and EC of irrigation water, respectively, and EC_d is the EC of the drainage water. This equation was used with measurements taken at 24-h intervals, In a separate trial, a comparison was made between E values calculated according to this equation, and measured values obtained by pot weighing and subtracting the quantitatively collected drainage water. The acceptable agreement between the methods (Calculated transpiration = 1.12× measured transpiration + 1.616, r^2= 0.79), gave confidence in the method, so that transpiration could be estimated throughout the growth period without daily weighing of pots.

Tissue chloride content was determined by coulometric–amperometric titration (Cotolov, 1963) on water extracts of samples taken from dried and ground plant material. Other ions were analyzed on H_2SO_4 digests of dried leaf samples: Na^+ and K^+ by flame photometry and Ca^{2+} by atomic absorption spectrophotometry.

All measurements were conducted on five replicate plants per treatment grown in different pots. Standard errors of the means are presented in figures and tables.

Results

In both cultivars, total leaf dry weight and total leaf area decreased with increasing salinity (Fig. 1). The rate of decline in these two components of growth was greater in H65-7052 than in H69-8235 mainly at the two highest levels of salinity imposed. In H65-7052, the relative decrease in leaf area under salinity was larger than that of dry weight, causing its specific leaf weight to increase (Fig. 1c), while that of H69-8235 remained nearly constant.

The responses of total leaf dry weight and area to salinity were further analyzed by calculating the average area of all the mature leaves and the number of leaves per plant (Fig. 2). While the average area per leaf was significantly reduced under salinity in H65-7052, it was hardly changed in H69-8235. The final number of mature green leaves was reduced in both cultivars but much more in the tolerant cultivar H69-823 5 than in the sensitive H69-7052. The formation of mature leaves was inhibited by salinity more strongly in H69-8235 than in H65-7052 (Table 1). While in H69-8235 the inhibition was already remarkable after 14 days, it could be seen only much later in H65-7052. This decrease in leaf number can mainly be attributed to enhanced rates of senescence of mature leaves, since the rate of leaf initiation was similarly inhibited by salinity in both cultivars.

Leaf water potential (Ψ_w) gradually declined during the first 30 days after salinization. Thereafter, a steady state was attained, except in the 12-dS/m treatment, where Ψ_w continued to decrease. It is interesting to note that Ψ_w of H69-8235 control leaves was lower than that of H65-7052 by 0.10–0.15 MPa (Fig. 3). Water potential decreased under salinity in H69-8235 approximately 0.2–0.3 MPa more than in H65-7052 at the high EC levels.

Daily transpiration rates per plant, per leaf and per unit leaf area were calculated according to Eq. (1) and are presented for the last 10 days of the experiment, when the changes in transpiration due to changes in leaf area were minimal (Fig. 4). The relative repression of transpiration by salinity was the least when calculated per unit leaf area and was maximal

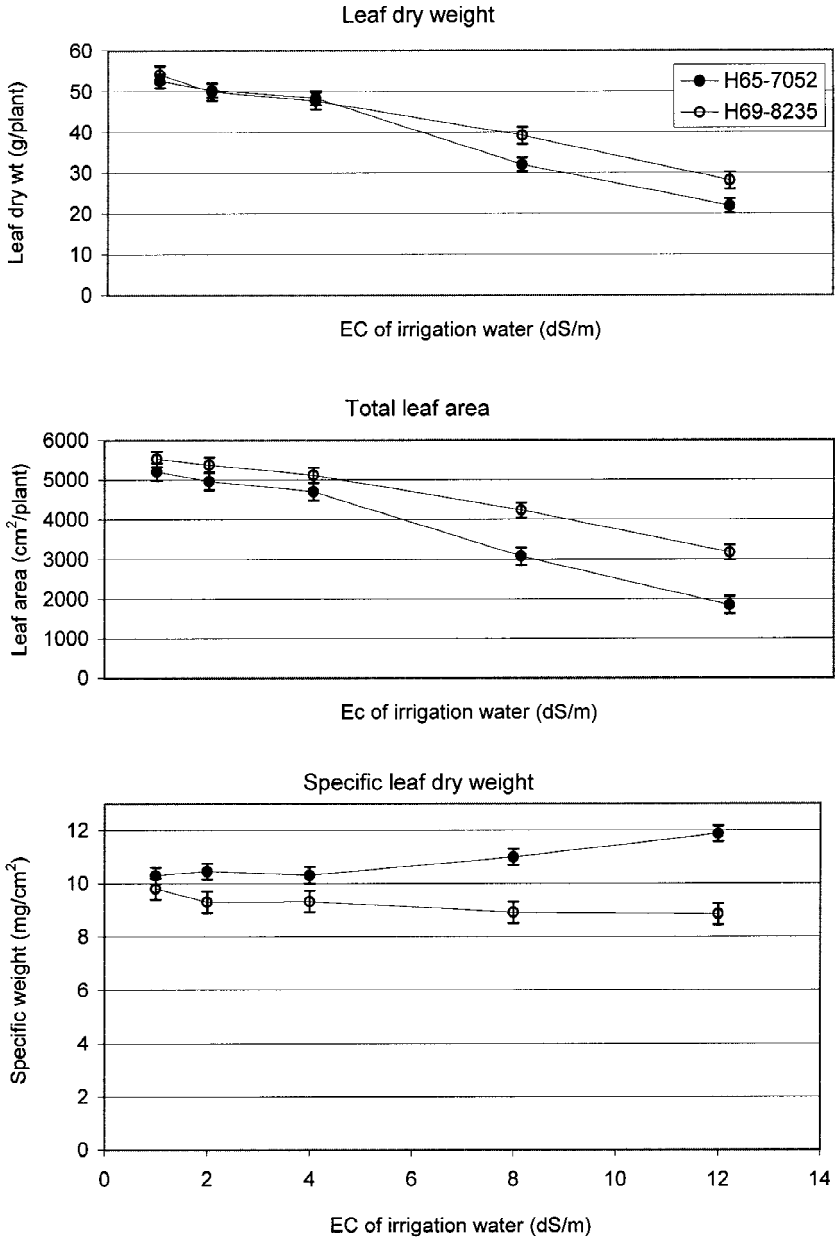

Figure 1. Effect of salinity on leaf dry weight per plant, leaf area per plant and specific leaf dry weight. Vertical bars present SE of the means, $n = 5$.

per plant, indicating that leaf development and growth were more sensitive to salinity than transpiration. The repression in transpiration of H65-7052 was stronger than that of H69-8235 on the basis of all parameters. There was a distinct rise in Cl and Na concentrations in the TVD leaves in both cultivars dependent on the external salinity during the initial 15 days (Table 2). An additional rise in concentration of both ions was then found mainly in H69-8235. It should be noted that the rise does not represent ion accumulation with time, since each measurement was conducted on a new TVD leaf present at the sampling date. It should be noted that the concentration of K was approximately 3 times that of Cl and that of Na was 1/10 of Cl. There was only a slight rise of leaf K at the high salinity levels,

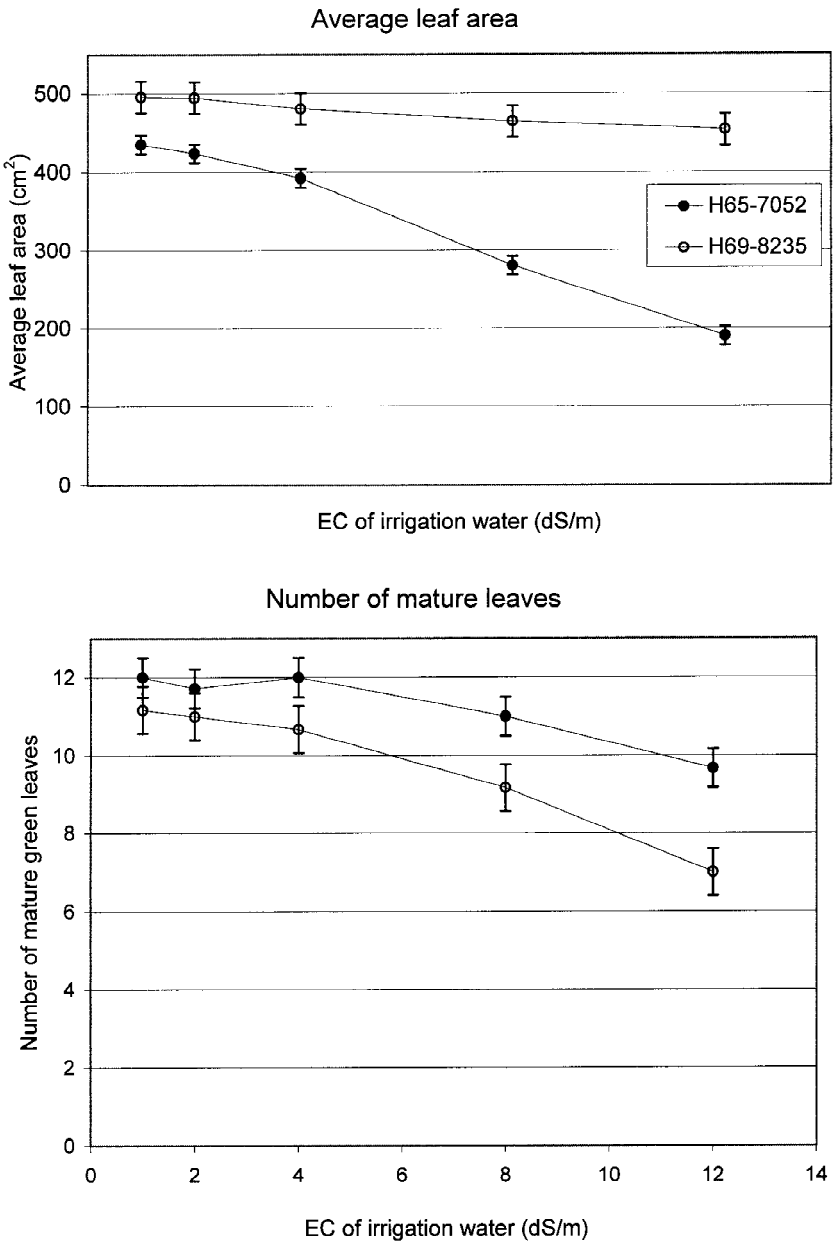

Figure 2. Effect of salinity on average area of individual leaves and on average number of mature green leaves per plant. Vertical bars present SE of the means, $n = 5$.

and a tendency for its concentration to decrease with time regardless of salinity level.

The distribution of Cl and Na among leaves was determined at the termination of the experiment and is presented for low, medium and high salinity levels (Table 3). In both cultivars, Cl and Na concentrations were lowest in the TVD-2 (expanding) leaf and increased with leaf age. However, the difference in ion concentration between the TVD leaf and the fourth leaf below it (which was still a fully green leaf) was much higher than between expanding and TVD leaves. It is of interest that the rise in leaf Cl as a function of external salinity was only remarkable in mature leaves, while the rise in Na was found in all leaves. Since Na concentrations were so low, even at the highest levels of external salinity, their physiological signific-

Table 1. Average number of mature green leaves and rate of new leaf initiation in cultivars H65-7052 and H69-8235 at different days after plant exposure to salinity: SE of the means in parenthesis, $n = 5$

	H65-7052 (sensitive)		H69-8238 (tolerant)	
Ec(dS/m)	14 days	63 days	14 days	63 days
(A) Leaf number: Average number of leaves on day 0 was 6.5 (0.3) in H65-7052 and 6.3 (0.2) in H69-8238				
1.0	7.6 (0.3)	12.0 (0.4)	7.7 (0.3)	11.2 (0.3)
2.0	7.9 (0.3)	12.2 (0.4)	7.5 (0.3)	11.0 (0.3)
4.0	7.7 (0.3)	11.8 (0.4)	6.9 (0.2)	10.6 (0.3)
8.0	7.4 (0.3)	10.9 (0.4)	6.1 (0.4)	9.3 (0.4)
12.0	7.3 (0.3)	9.7 (0.3)	5.6 (0.2)	7.0 (0.2)
(B) Number of new leaves formed per day				
1.0	0.118 (.006)	0.137 (.008)	0.140 (.003)	0.151 (.004)
2.0	0.135 (.006)	0.122 (.006)	0.135 (.010)	0.128 (.008)
4.0	0.100 (.010)	0.091 (.010)	0.122 (.005)	0.112 (.006)
8.0	0.079 (.003)	0.083 (.005)	0.083 (.012)	0.075 (.012)
12.0	0.067 (.002)	0.068 (.002)	0.068 (.003)	0.090 (.003)

ance was uncertain. The possibility that a specific Na effect was responsible for the decrease in leaf growth, and transpiration was evaluated on the basis of the second experiment, conducted in nutrient solutions. This was mainly to avoid a possibility of Na adversely affecting soil structure and aeration, and as soil was a major component of the mixture, aeration of the entire mixture and oxygen supply to the root system could be rate limiting. In both cultivars, no specific effect of Na on final leaf area was observed (Table 4). There was a decrease in transpiration rate as a function of EC, mainly at the high EC level, but no specific Na effect was detected. Transpiration rates were determined at the age of 60 days when the EC was 3 dS/m, and again at the age of 90 days when EC was 6 dS/m, while leaf areas are presented only for the end of the experimental period.

In both cultivars, the distribution of Cl among leaves, stalks and roots was uniform throughout the plant in the control unsalinized plants (Fig. 5). Under salinity, however, Cl concentration in the roots increased by 6-7-fold and only by 1.5-2.5-fold in the leaves and stalk. The accumulation of ions in the roots was most remarkable in the case of Na, in which differences in accumulation at the two Na:Ca ratios were clearly observed. In contrast, the K concentration was significantly higher in the leaves and stalks as compared with roots. It is noteworthy that the high Na:Ca ratio induced an increase in stalk K concentration mainly in H65-8235. The concentration of Ca in roots of both cultivars was 4-5-fold higher than in the leaves of control plants, and sharply increased in both organs at low Na:Ca ratio. At high Na:Ca ratio, the concentration of Ca was reduced compared with the controls mainly in the roots. It is interesting that Ca concentration in the stalk was low and was hardly affected by salinity or by Na:Ca ratio.

Discussion

The basis of the higher salinity tolerance of the sugarcane cultivar H69-8235 compared with other high-yielding sugarcane cultivars is not known. The number of mature leaves was smaller in this cultivar than in H65-7052 at all salinity levels, due to enhanced rates of leaf senescence and injury (Fig. 2 and Table 1). In spite of this, total plant leaf area and dry weight were greater in H69-8235 than in the less tolerant H65-7052 over the entire salinity range imposed (Figs. 1 and 2). Rates of leaf expansion and new leaf formation (Table 1), known to be salinity sensitive (Bernstein et al., 1993; Crane and Bowman, 1991; Greenway and Munns, 1980; Lewis et al., 1989; Meiri et al., 1992), were indeed inhibited by salinity to a lesser extent in H69-8235 than in H65-7052.

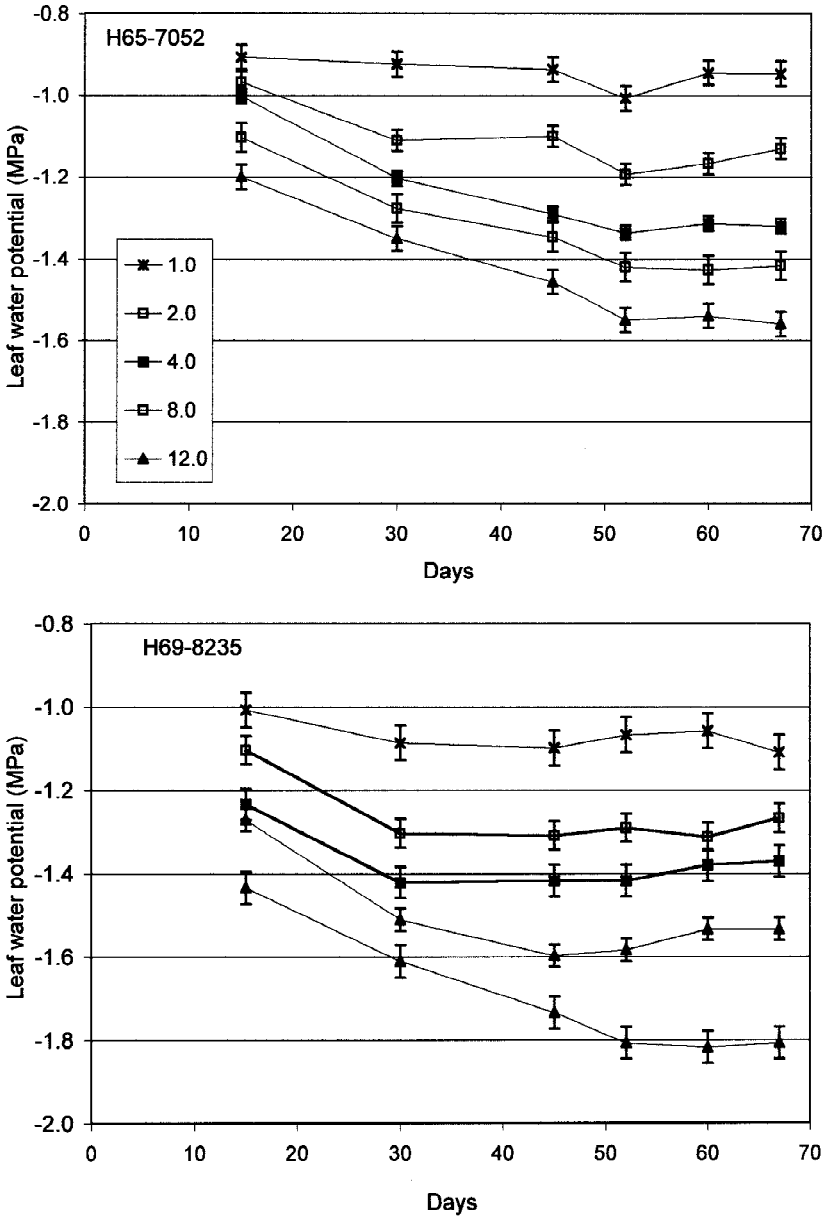

Figure 3. Effect of salinity on leaf water potential, as determined throughout the experimental period. Vertical bars present SE of the means, *n* = 5.

Stomatal conductance of the more salinity-tolerant H69-8235 was previously found to be higher than that of the more sensitive H65-705 2 (Meinzer et al., 1994), implying that the transpiration rate should be higher in the tolerant cultivar as confirmed in the present study (Fig. 4). The higher stomatal conductance of H69-8235 could either be due to higher stomatal density, small anatomical differences, a lower response of guard cells to stress, or a combination of all factors. The higher leaf conductance led to the higher transpiration rate (Fig. 4) in H69-8235. It may be expected that it would induce more negative leaf water potential than in H65-7052 if hydraulic properties of the two cultivars were smiilar. The pattern shown in Fig. 3 appears to be consistent with this prediction, especially at the high salinity levels. An estimate of the total root/leaf hydraulic conductance can be obtained by dividing the transpiration rate per unit leaf area (Fig.

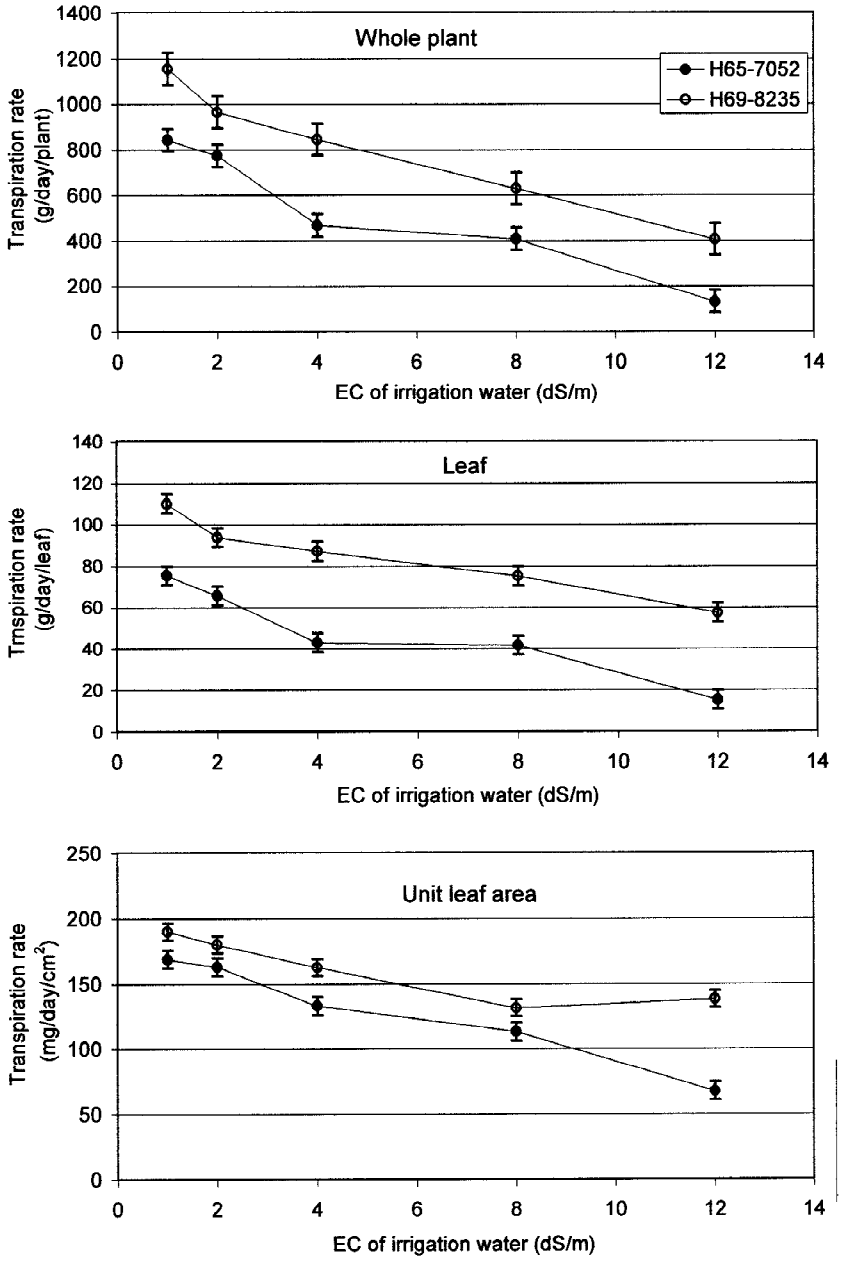

Figure 4. Effect of salinity on transpiration rates by sugarcane plants during the last 10 days of the experiment, as determined on the whole-plant, single leaf and unit of leaf area basis. Vertical bars present SE of the means, $n = 5$.

4) by leaf water potential (Fig. 3). It was found that hydraulic conductance was about 50% greater in H69-8235 than in H65-7052 at the highest salinity level. Maintenance of greater hydraulic conductance in H69-8235 under increasing salinity thus greatly reduced the impact of its higher transpiration rate on leaf water potential at the highest salinity levels. Hydraulic conductance of the two cultivars was, however, nearly equal in the control treatment.

The concentration of Na in the leaves was only a approximately 1/10 of that of Cl at all salinity levels. This can mainly be interpreted by retention of Na by the media outside the root system or within the roots and stalk. In-fact, both cultivars were very efficient in

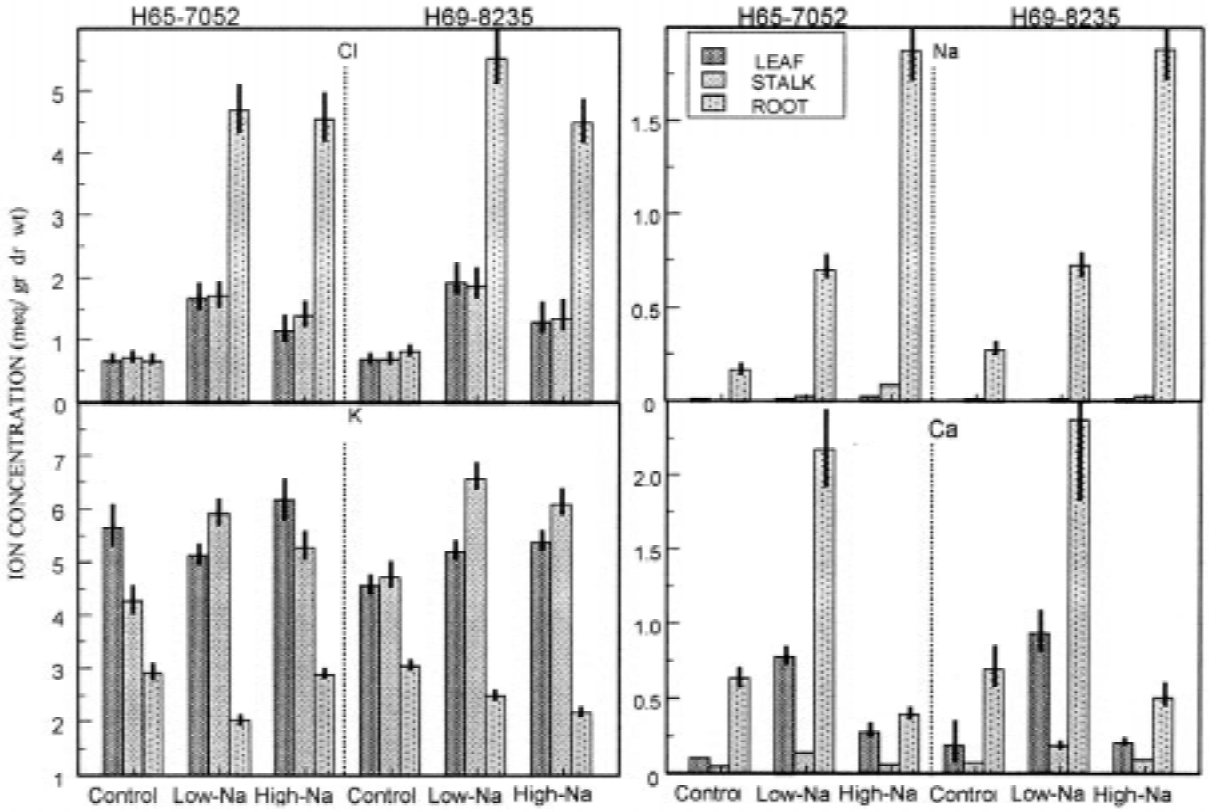

Figure 5. Effect of relative sodium concentration in the salinized nutrient solution on ion concentrations in sugarcane leaves, stalks and roots. Vertical bars present SE of the means, $n = 5$.

Table 2. Concentration of leaf CI, Na and K (in μmol per gram dry weight) of cultivars H65-7052 and H69-8235 after 15 and 60 days of irrigation with water of different salinity levels. Ion concentrations at the onset of treatments were: 173 and 225 for Cl, 12 and 16 for Na and 588 and 688 for K in H65-7052 and H69-823, respectively.

		Na		Cl		K	
Cultivar	EC	15 days	60 days	15 days	60 days	15 days	60 days
H65-7052	1.0	12.5	10.1	183	200	550	463
(sensitive)	2.0	13.3	11.0	194	211	625	476
	4.0	12.9	12.1	204	216	551	481
	8.0	13.9	14.7	218	225	538	500
	12.0	14.2	15.9	253	266	663	575
H69-8235	1.0	15.8	17.3	230	278	538	475
(tolerent)	2.0	16.5	17.8	262	323	600	455
	4.0	16.7	18.6	270	333	563	426
	8.0	18.4	19.1	284	339	663	487
	12.0	20.9	22.8	320	362	712	524

exclusion of Na from the stalk and more noticeable from the leaves (Fig. 5). Moreover, a 36-fold rise in the Na:Ca ratio in the externally applied salts had no effect on growth or on transpiration (Fig 5 and Table 4). This may be interpreted by the possible exclusion of Na from sugarcane leaves. Relatively high concentrations of all ions, especially Na, were found in the root, although their specific compartmentation was not determined. This behaviour was more accentuated in H69-8235.

The most evident effect of salinity is disturbances in plant growth. The accepted definition of growth is irreversible increase in size through cell and organ extension. The response of leaf growth to salinity is, therefore, mostly considered as a reduction in its expansion (Lazof,1991; Plaut and Heuer, 1985; Poljakoff-Mayber, 1993; Saliendra et al., 1990; Wignarajah, 1990). Turgor pressure, which is the driving force for extension growth, must exceed the yield threshold of cell walls in order to enable growth and, subsequently, osmotic adjustment is a prerequisite for leaf expansion under salinity. The higher salt tolerance

Table 3. Dependence of Cl and Na concentrations in sugarcane leaves on leaf age, cultivar and EC of the irrigation water. (TVD-2, TVD,and TVD+4 are second leaf above TVD leaf, TVD leaf and forth leaf below TVD leaf). Ion concentrations were determined at termination of experiment and are expressed as μg equivalent per g dry weight. SE of the means are in parenthesis, n=5.

		EC(ds/m)					
		Na			Cl		
Cultivar	Leaf	1	4	12	1	4	12
H65-7052	TVD-2	7.8	10.6	14.7	162	187	202
(sensitive)		(1.1)	(1.7)	(1.9)	(12)	(11)	(9)
	TVD	9.7	12.3	15.5	202	215	220
		(0.8)	(2.2)	(2.1)	(16)	(8)	(15)
	TVD+4	12.6	21.3	26.4	275	436	505
		(1.4)	(2.0)	(2.0)	(11)	(31)	(14)
H69-8235	TVD-2	9.4	12.2	13.1	209	256	239
(tolerent)		(0.5)	(0.5)	(0.5)	(19)	(12)	(16)
	TVD	11.7	12.8	17.2	283	330	359
		(0.10)	(0.9)	(0.9)	(21)	(29)	(27)
	TVD+4	18.6	24.1	28.8	412	481	614
		(1.9)	(1.4)	(0.8)	(39)	(17)	(49)

Table 4. Effect of relative sodium concentration in the nutrient solution on final leaf area and on transpiration rates per plant at two EC levels. Standard errors of the means are in parenthesis.

	Leaf area (cm^2)			
	H65-7052 (sensitive)		H69-8235 (tolerant)	
Control	3259 (374)		3879 (401)	
Low Na:Ca	1740 (226)		2159 (205)	
High Na:Ca	2165 (258)		2380 (211)	
	Transpiration rate (g/plant/h)			
	H65-7052 (sensitive)		H69-8235 (tolerant)	
	3 dS/m	6 dS/m	3 dS/m	6 dS/m
Control	92.6 (8.2)	84.6 (8.0)	119.1 (10.3)	112.3 (10.7)
Low Na	73.7 (7.0)	42.1 (4.8)	109.1 (10.1)	57.9 (6.3)
High na	68.0 (6.9)	49.3 (5.1)	109.0 (9.8)	65.4 (6.7)

of H69-8235 which is evident from the more limited decrease in leaf area under salinity as compared with H65-7052, must therefore be a result of its osmotic adjustment and turgor maintenance. Such turgor maintenance was probably achieved partly by uptake and accumulation of ions within leaf cells and partly by accumulation of organic solutes (Kumar et al., 1988). The ion, which most substantially increased under salinity, was Cl (Figs. 6 and 7). Dry matter content of a mature TVD leaf was 13.5% in the control (EC=l dS/m) and was gradually increase by salinity up to 17% at the highest salinity level. Based on Table 2, the rises in Cl concentrations in the leaf water above that of the control were 11,16,22 and 30 mEq/l at the four externally elevated salinity levels in H69-8235. The rises in H65-7052 were only 4, 6, 10 and 18. The increments of Cl concentration in the irrigation water were 9, 27, 63, and 100 mEq/l for these treatments. Although the distribution of Cl between apoplast and symplast was not directly determined, it is clear that the contribution of Cl to osmotic adjustment was only partial, in contrast to what was found for more salt tolerant plants, like cotton (Plaut and Federman, 1991). The possible role of wall extensibility and yield threshold cannot be excluded, however.

The enhanced growth rate in H69-8235, as compared with H65-7052 at equal salinity levels, was also evident at the leaf initiation stage and resulted in higher rates of leaf appearance (Table 1). Longer intervals between the appearance of individual leaves as a result of salinity has also shown for other crops like sorghum (Bernstein et al., 1993) and lettuce (Lazof et al., 1991), but no evidence is available on the relationship between this phenomenon and salinity tolerance.

In conclusion, the findings of the present study indicate that both sugarcane cultivars could still tolerate EC levels up to 8 dS/m, although this was associated with a decrease in growth and transpiration. The higher salinity tolerance of H69-8235 can be interpreted on the basis of its higher hydraulic conductivity resulting in a higher transpiration rate, not associated with lower leaf water potential. An efficient exclusion of Na from leaves. The transport of other ions to the leaves could assist in their osmotic adjustment.

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