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Differential Effects of Sodium/Calcium Ratio on Sorghum Genotypes

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ABSTRACT

Plant response to salinity is a function not only of the total salt concentration but also of the Na/Ca ratio in the root medium. Calcium transport to the shoot decreases at high external Na/Ca and, in many gramineous species, Ca concentration in the expanding blades may become deficient. This study was initiated to determine the differential susceptibility of sorghum [*Sorghum bicolor* (L.) Moench] genotypes 'NK 265', 'NB 9040', and 'Hegari' (PI 34911) to the Na/Ca ratio in solution cultures. Plants were grown in the greenhouse with six Na/Ca ratios at two salinity levels (osmotic potentials = −0.4 and −0.6 MPa.) NK 265 and NB 9040 were sensitive to high Na/Ca molar ratios at both salinity levels (Na/Ca = 34.6 at −0.4 MPa and 52 at −0.6 MPa). Shoot growth was inhibited; blade injury was typical of severe Ca deficiency. In contrast, at −0.4 MPa, Hegari grew best at high substrate Na and the seedlings had no Ca deficiency symptoms. The K:Na selectivity ratios in Hegari shoots were lower than those in either NK 265 or NB 9040 shoots. The tolerance of Hegari to high external Na was attributed to efficient Ca transport to the developing blades. At both salinity levels, low Na/Ca ratio significantly reduced dry matter yield of Hegari shoots. In all three genotypes, shoot Na decreased with decreasing Na/Ca and was preferentially accumulated in the sheaths. The diversity of the sorghum genotypes in their response to external Na/Ca may be utilized by plant breeders to develop a line that is suited to sodic soil conditions.

Additional Index Words: **Calcium deficiency, Potassium/sodium selectivity, Salinity stress, *Sorghum bicolor* (L.) Moench.**

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STUDIES OF SALT-AFFECTED SOILS have shown that increases in exchangeable Na, accompanied by decreases in exchangeable Ca, may result in ion imbalances that adversely affect plant growth. High external Na reduces the activity of Ca ions in the root medium and decreases the amount of Ca that is available for uptake by the plant (Cramer and Läuchli, 1986; Cramer et al., 1986). Calcium concentrations that are adequate under nonsaline conditions may become nutritionally inadequate when the external Na/Ca ratio is high (Bernstein, 1975). Root growth and function may be inhibited, and the processes whereby Ca is transported from root to shoot may be impaired (Lynch and Läuchli, 1985). The cereals are particularly susceptible to Ca deficiency at high external Na/Ca ratios. Sodium-induced Ca deficiency symptoms have been observed in sorghum (Kawasaki and Moritsugu, 1979), corn (*Zea mays* L.) (Maas and Grieve, 1987), rice (*Oryza sativa* L.) (Grieve and Fujiyama, 1987), and barley (*Hordeum vulgare* L.) (Maas and Grieve, unpublished data). The cereals show striking intergeneric differences in tolerance to saline cultures of equal osmotic potential (OP) with different molar ratios of Na and Ca. A salt stress of −0.6 MPa and Na/Ca = 52 reduced the relative dry matter yield of wheat (*Triticum aestivum* L., 'Probred' and 'Inia') less than that of rye (*Secale cereale* L., 'Merced'), or oat (*Avena sativa* L., 'Curt' and 'Swan') (Maas and Grieve, unpublished data). At −0.4 MPa, rice ('M-201') was more sensitive at Na/Ca = 5 than was the corn 'Pioneer 3906' (Grieve and Fujiyama, 1987; Maas and Grieve, 1987).

This paper describes a comparative study of the response of three sorghum genotypes to a wide range of Na/Ca ratios in nutrient cultures maintained at one of two salinity levels (−0.4 or −0.6 MPa). Differential responses are described with respect to dry matter production, visual symptoms of ion toxicity or deficiency injury, and distribution of elements in shoot organs.

MATERIALS AND METHODS

The genotypes of grain sorghum selected for this study were: NK 265, a commercial hybrid; Hegari (PI 34911), a member of the race caudatum (Harlan and deWet, 1972); and NB 9040, an inbred line obtained from the University of Nebraska.

Seeds were soaked in aerated, dilute $CaSO_4$ (0.1 mol m^{-3}) for 4 h, then germinated in the dark (Tanada, 1962). Uniform 2-d-old seedlings were placed on cheesecloth supported between two plastic grids with 1.7-cm^2 openings, then covered with moist vermiculite. The grids were taken to the greenhouse and suspended over pots containing 28 L of continuously aerated nutrient solution so that the seedling roots were immersed in the solution. The composition of the nutrient solution in mol m^{-3} was: 2.5 $Ca(NO_3)_2$, 3 KNO_3, 1.5 $MgSO_4$, 0.17 KH_2PO_4, 0.05 Fe (as sodium ferric diethylenetriamine pentaacetate), 0.023 H_3BO_3, 0.005 $MnSO_4$, 0.0004 $ZnSO_4$, 0.0002 $CuSO_4$, and 0.0001 H_2MoO_4. The pH of the solution was maintained between 5.0 and 6.0 with H_2SO_4 and KOH. Air temperatures in the glasshouse are given in Table 1.

Eight days after germination, the plants were thinned to 75 seedlings per pot and salination was initiated. Salts were added at a rate calculated to reduce the osmotic potential by 0.2 MPa d^{-1}. Specific treatments are shown in Table 2. Pots were arranged in a randomized block design with three or four replications. Each experiment included at least three pots of nonsalinized plants. All solutions were changed twice weekly. Water was replenished daily.

Table 1. Dates of germination and glasshouse temperatures for growth of sorghum at two levels of salt stress.

Sorghum genotype	Date of germination	Osmotic potential	Temperature Maximum	Temperature Minimum
		MPa	°C	°C
NK265	16 May 1983	−0.6	34.5	21.7
	21 May 1984	−0.4	37.7	21.8
Hegari	27 June 1983	−0.6	33.4	22.5
	21 May 1984	−0.4	37.7	21.8
NB9040	27 Aug. 1984	−0.4	35.5	21.8
		−0.6	35.5	21.8

Table 2. Sodium and Ca composition in the nutrient cultures for sorghum at two levels of salt stress.

−0.4 MPa Na	−0.4 MPa Ca	−0.6 MPa Na	−0.6 MPa Ca
mol m^{-3}			
86.5	2.5	130.0	2.5
71.3	12.6	108.2	17.8
57.1	22.2	86.5	34.0
43.1	34.0	64.8	49.0
28.2	44.0	43.1	66.0
14.1	54.6	21.4	80.2

At 5- to 7-d intervals after salination, plants were randomly harvested. Twenty to 30 shoots were sampled from each pot in the early harvests; 10 to 12 shoots were taken in the final harvest. For treatments at −0.4 MPa, the final harvest took place 37 d after salination when the seedlings were 45 d old and the unsalinized control plants had reached Growth Stage 4 (Vanderlip and Reeves, 1972). For the experiments at −0.6 MPa, the seedlings were 30 d old (22 d after salination) and the growth stage of the controls was approximately 3.5. The shoots were visually examined for symptoms of nutrient deficiency or toxicity. Shoots with blades that were either dead or tightly curled (swordlike) or deeply serrated were rated as severely Ca deficient (Clark, 1984). Mild Ca deficiency was characterized by blades that were very shallowly serrated and/or by short withered tips (<5% of the total blade length). The shoots were weighed and separated as follows: mature blades, sheaths including culm, and immature and unexpanded blades. The tissues were oven-dried at 75 to 80 °C for 1 wk, reweighed, and ground in a blender.

Sodium, K, Ca, and Mg were determined on nitric-perchloric acid digests of the plant tissues by atomic absorption spectrophotometry.

The K:Na selectivity ratios ($S_{K,Na}$) were calculated following Pitman (1976):

$$S_{K,Na} = \text{(K content/[K] medium):(Na content/[Na] medium)}$$

RESULTS

Shoot Growth and Injury

At both salinity levels, the sorghum genotypes were sensitive to the Na/Ca ratio in the root medium. Pronounced genotypic differences were apparent both in dry matter production and in blade injury symptoms. Shoot dry weights of seedlings grown for 37 d in nutrient cultures salinated at −0.4 MPa are shown in Fig. 1. The Na/Ca ratio had a significant effect on dry matter production of Hegari and NB 9040 but not of NK 265 at −0.4 MPa (Table 2). Hegari shoots salinated at −0.4 MPa showed no visual indications of nutrient imbalance and maintained healthy growth.

Both NK 265 and NB 9040 grown at −0.4 MPa were sensitive to high Na/Ca ratio. The decrease in dry matter production of NB 9040 (Fig. 1) was the result of blade injury in a pattern that is characteristic of Ca deficiency in cereals (Clark, 1984; Kawasaki and Moritsugu, 1979; Maas and Grieve, 1987). Severe injury also occurred on NK 265 blades at Na/Ca = 34.6, however, a slight increase in the growth of the sheath and culm tissues made the total effect on dry matter production insignificant. Injury was initially observed on the emerging sixth leaf. At the first harvest, 9 d after salination was complete, severe injury was observed on all of the NB 9040 shoots (n = 45) and 76% of the NK 265 shoots (n = 60) harvested from cultures with Na/Ca = 34.6. No injury was observed on NB 9040 blades in any other treatment at −0.4 MPa, while a few individual NK 265 plants were at least mildly affected at all Na/Ca ratios.

Dry matter production of the three genotypes grown at −0.6 MPa was compared at 22 d after salination (Fig. 2, Table 3). The experimental period was limited by the performance of NK 265. This genotype was

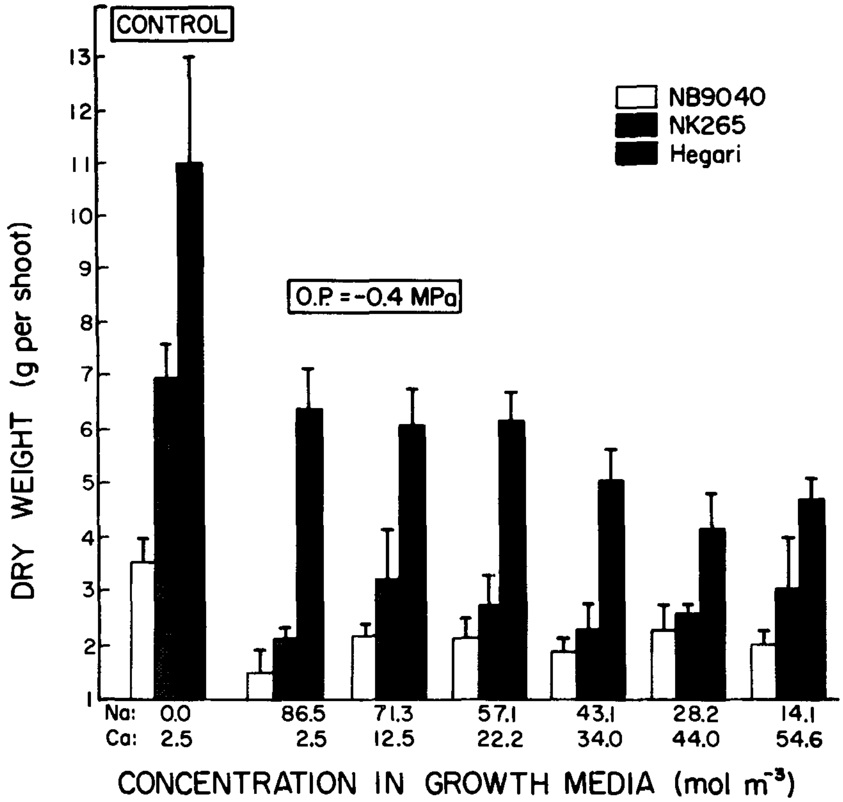

Fig. 1. Dry shoot yields of 45-d-old plants of three sorghum genotypes as a function of Na/Ca ratio in the root media. Plants salinized on Day 8. Data are means of three replications with SD.

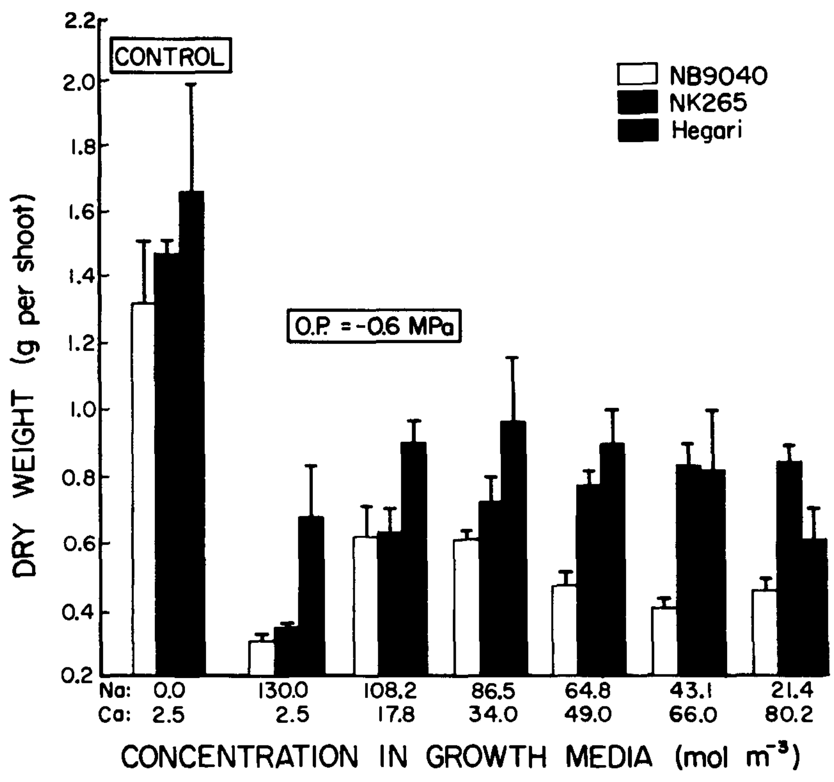

Fig. 2. Dry shoot yields of 30-d-old plants of three sorghum genotypes as a function of Na/Ca ratio in the root media. Plants salinized on Day 8. Data are the means of three replications with SD.

acutely sensitive to the Na/Ca ratio of 52; the plants did not survive this treatment for more than 24 to 26 d. Severe blade injury was observed at all Na/Ca ratios, but the number of damaged shoots decreased with decreasing Na/Ca. Nine days after salination, 88% of the shoots harvested from cultures with Na/Ca = 52 were severely damaged, while 36, 18, and 10% of the shoots harvested from cultures with Na/Ca ratios of 6.1, 2.5, and 1.3, respectively, were affected (n = 120 shoots per treatment).

NB 9040 was heavily damaged, but not killed, by

Table 3. Analysis of variance of shoot dry weights of sorghum as a function of Na/Ca ratio.

		Osmotic potential					
		−0.4 MPa‡			−0.6 MPa§		
		Genotypes					
Source	df	NK265	NB9040	Hegari	NK265	NB9040	Hegari
		F values					
Na/Ca ratio	5	0.86	4.04*	5.98**	13.12†	9.70†	2.06
Linear	1	1.33	14.3†	11.52**	59.01†	18.08†	1.83
Quadratic	1	1.09	1.23	9.12*	6.08*	23.33†	3.15
Cubic	1	1.02	0.053	5.31*	0.38	3.36	4.26
Error mean square	10	0.5999	0.0644	0.437	0.00774	0.00454	0.0293

*,**,† Significant at the 0.05, 0.01, and 0.005 level of probability, respectively. Values from nonsalinated control plants are not included in this analysis.

‡ Harvested 37 d after salination.

§ Harvested 22 d after salination.

Fig. 3. Calcium deficiency symptoms on NB 9040 seedling salinized with NaCl (130 mol m^{-3}; Na/Ca = 52; OP = −0.6 MPa).

Na/Ca = 52 (Fig. 3 and 4). In contrast, only 20% of the Hegari seedlings showed mild to moderate Ca deficiency symptoms at Na/Ca = 52. Neither Hegari nor NB 9040 developed visible injury symptoms at any other Na/Ca ratio.

A unique, genotype-dependent pattern of Ca distribution was exhibited in the tissues of nonstressed 45-d-old sorghum seedlings (Fig. 5). Calcium concentration in the young blades of nonsalinated NK 265 and NB 9040 were 25 to 30% of those in the mature leaves. In contrast, the Ca concentration in immature blades of Hegari was 65% of that in the older tissue. The relationship between Ca concentration in the mature blades and the sheaths, including culms, of Hegari and NB 9040 that existed under nonsaline conditions was maintained at all Na/Ca ratios at −0.4 MPa. Calcium accumulation by the mature blades of Hegari was greater than in the sheaths; the reverse was true for NB 9040 shoots. At Na/Ca = 34.6, the younger blade tissue of NK 265 was the most reliable indicator of the Ca status of the shoots. Calcium concentrations in the mature NK 265 blades, even those that had initially shown lesions of Ca deficiency, were as high as those in the nonsalinated blades.

At Na/Ca = 34.6, the Ca concentration in the youngest blades of all three genotypes was reduced below the level in the nonsalinated tissue. Although large increases in external Ca concentration substantially increased Ca accumulation by the mature portion of the shoot, Ca in the immature blades increased only slightly.

At an OP of −0.6 MPa and Na/Ca = 52, Ca concentrations in the youngest blades of all cultivars were reduced to approximately one-half of those in the corresponding nonsalinated tissues (Fig. 6). Salt stress had no effect on Ca accumulation by the mature blades of NK 265 when the Na/Ca ratio was high (34.6 or 52). As the external Na/Ca decreased, Ca increased in the immature blades of all three genotypes.

Sodium concentration in the sorghum shoots decreased in response to decreasing Na/Ca ratios (Fig. 5 and 6)., At both salinity levels, Na was preferentially retained in the sheaths and excluded from the youngest blades of NK 265 and NB 9040. This pattern was also exhibited by Hegari salinated at −0.4 MPa. At −0.6 MPa, however, Na accumulation was higher in all Hegari tissues and its distribution differed from that in NK 265 and NB 9040. As the Na/Ca ratio increased from 34.6 at −0.4 MPa to 52 at −0.6 MPa, Na concentration in the immature blades increased by nearly two orders of magnitude, while in the older blades and sheaths it increased by seven- and twofold, respectively. At −0.6 MPa, Na exclusion from the young Hegari blades occurred only at the lowest Na/Ca ratio (0.3).

Potassium concentrations in mature blades were decreased at both −0.4 and −0.6 MPa, but the genotypes were affected differently in response to decreasing external Na/Ca (Table 4). Potassium concentration in NK 265 decreased slightly, but the effect was significant only at −0.6 MPa; whereas in NB 9040, K decreased significantly at both salinity levels. The K concentrations in Hegari were not affected by Na/Ca ratio at either salinity level.

The K/Na ratios and the $S_{K,Na}$ values for whole shoots of the 45-d-old sorghum plants grown at −0.4

MPa are given in Table 5. The K/Na ratios increased substantially for all three genotypes as the substrate Na concentration decreased. As expected, the $S_{K,Na}$ increased with decreasing external Na/Ca; however, in NK265 and Hegari, it tended to decrease at Na/Ca < 1.3

At both salinity levels, Mg accumulation in the mature blades of NK 265 and NB 9040 was stimulated by high substrate Na/Ca (Table 4), while Mg in Hegari blades increased at −0.4 MPa. Blade Mg of all three genotypes decreased significantly as external Ca increased.

DISCUSSION

The results of this study demonstrate that sorghum is sensitive to the Na/Ca ratio in saline root media. The distinctly different response patterns of the three genotypes, NK 265, NB 9040, and Hegari, were further influenced by OP of the nutrient cultures. At both

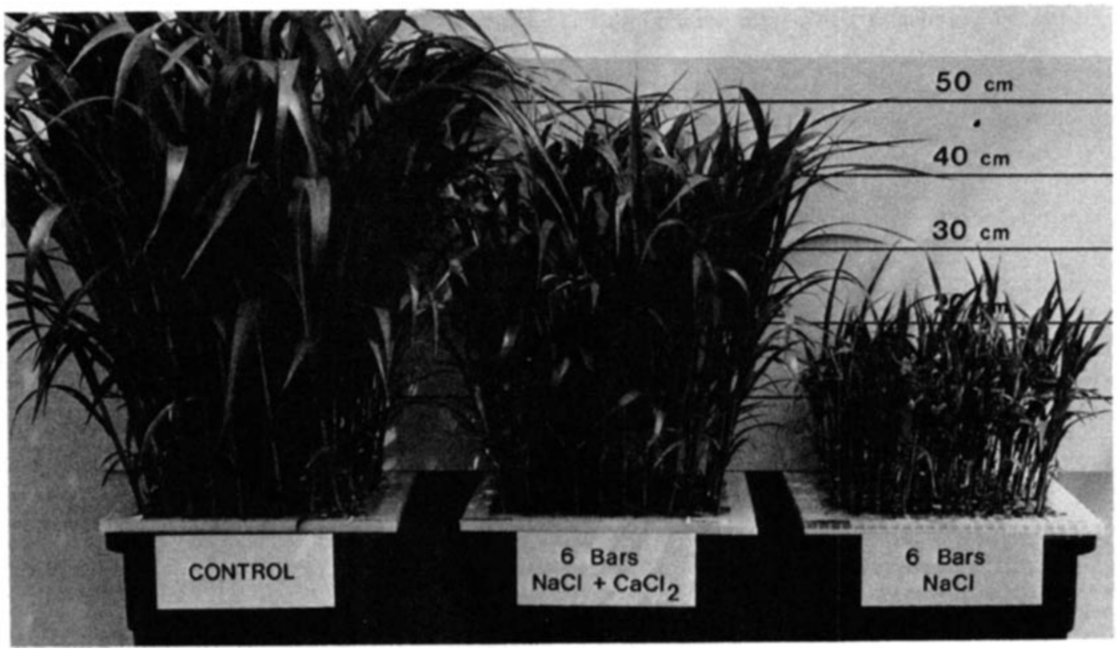

Fig. 4. Effect of iso-osmotic solutions (OP = −0.6 MPa) on growth of sorghum NB 9040. The nutrient solution in all pots contained 2.5 mol m^{-3} $Ca(NO_3)_2$. The Na/Ca ratio in center pot = 2, and in pot on the right Na/Ca = 52.

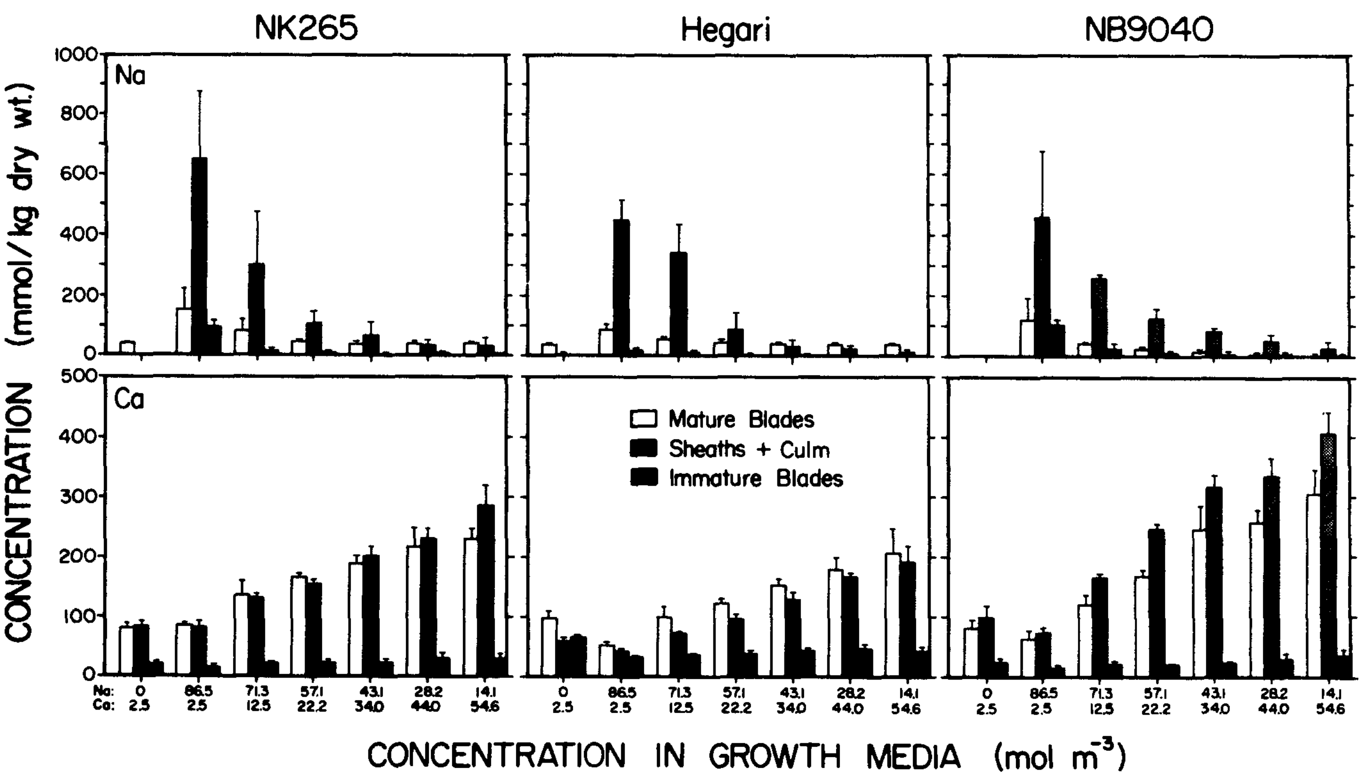

Fig. 5. Calcium and Na concentrations in 45-d-old sorghum seedlings as a function of Na/Ca ratio in the root media. The OP of the saline cultures = −0.4 MPa. Data are the means of three replications with SD.

−0.4 and −0.6 MPa, NB 9040 showed Ca deficiency symptoms only at the highest Na/Ca ratio. NK 265 was damaged to some extent by all Na/Ca treatments, but was most severely injured at the highest Na concentration. Although Hegari was tolerant of high Na/Ca, the reduction in growth at low Na/Ca suggests that high Ca concentrations may be toxic to this cultivar.

The sorghum genotypes showed important differences in their ability to absorb and to distribute Ca within the shoot. Hegari stressed at −0.4 MPa achieved optimum growth in cultures that were low in available Ca and was equally efficient in acquiring Ca from solutions with Na/Ca ratios ranging from 35 to 3. The pattern of Ca distribution in Hegari shoots undoubtedly contributed to the Ca efficiency of this cultivar. Substantial increases in substrate Ca resulted in increased Ca accumulation in the mature shoot tissues; Ca in the expanding blades remained relatively constant.

In NK 265 and NB 9040, shoot injury at Na/Ca = 34.6 was more closely related to inefficient Ca distribution than to insufficient Ca uptake. Sodium toxicity did not appear to be a major factor in the sensitivity of NK 265 to high Na/Ca. All three genotypes had the ability to limit Na transport to the youngest blades at −0.4 MPa. At −0.6 MPa, however, Na concentrations reached very high levels in the immature blades of Hegari while remaining relatively low in NK 265 and NB 9040. This observation suggests that NK 265 and NB 9040 have Na exclusion mechanisms, as yet uncharacterized, that remain effective even at OP =

Table 4. Potassium and Mg concentrations in mature blades of sorghum plants as a function of Na/Ca ratio in the growth media.

	K concentration			Mg concentration		
Na/Ca ratio	NK265	Hegari	NB9040	NK265	Hegari	NB9040
	mmol kg^{-1} dry wt.					
OP = −0.4 MPa						
Nonsaline control	947*	792*	975*	104*	151*	112*
34.6	740a	541a	771a	182a	144a	172a
5.7	750a	546a	762a	156b	125ab	126b
2.6	743a	550a	768a	147bc	111b	117b
1.3	687a	572a	613b	139c	99bc	90c
0.6	713a	625a	645b	134c	95bc	86c
0.3	653a	537a	617b	106d	70c	71c
	CV, % = 7.9			CV, % = 12		
OP = −0.6 MPa						
Nonsaline control	1254*	865*	1263*	154*	132*	138*
52.0	766ab	403a	601b	261a	80a	185a
6.1	799a	403a	730b	168b	47b	146b
2.5	699abc	401a	657b	141c	45b	112c
1.3	616bc	406a	531c	110d	41b	93d
0.6	603c	355a	478dc	95de	38b	86d
0.3	666bc	367a	433d	78e	38b	74d
	CV, % = 7.4			CV, % = 10		

* Control values were not included in analysis of variance. Values in columns within OP followed by the same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test. Means are the average of three measurements.

Table 5. The K/Na ratios and selectivity ($S_{K,\,Na}$) in sorghum shoots as a function of Na/Ca ratio in cultures salinized at −0.4 MPa.

Na/Ca ratio	NK265		Hegari		NB9040	
	K/Na	$S_{K,\,Na}$	K/Na	$S_{K,\,Na}$	K/Na	$S_{K,\,Na}$
34.6	2.5	68	1.6	43	4.1	111
5.7	6.4	144	2.3	52	7.0	158
2.6	13.4	241	11.0	199	14.4	259
1.3	21.6	294	22.2	302	15.6	213
0.6	32.0	285	26.8	239	28.3	251
0.3	29.2	130	30.5	136	65.6	292

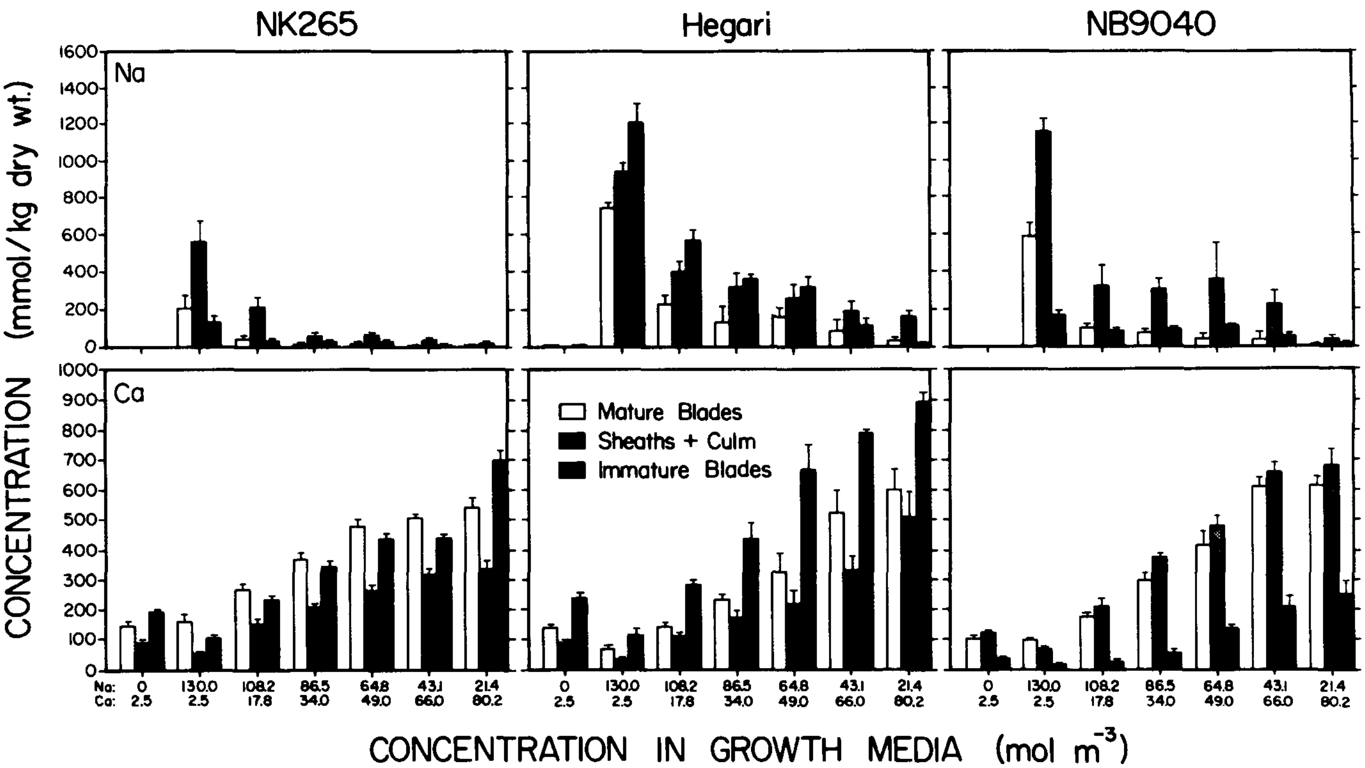

Fig. 6. Calcium and Na concentrations in 30-d-old sorghum seedlings as a function of Na/Ca ratio in the root media. The OP of the saline cultures = −0.6 MPa. Data are the means of three replications with SD.

−0.6 MPa and Na/Ca = 52. The ability to exclude Na was also reflected in the K:Na selectivity ($S_{K,Na}$) of the shoots. Both NK 265 and NB 9040, the genotypes most sensitive to high Na/Ca in the root media, maintained higher K selectivity than the more tolerant Hegari. At more intermediate Na/Ca ratios (1.3 and 2.6), $S_{K,Na}$ of the three genotypes were similar despite the greater salt tolerance of Hegari.

Hegari is relatively unchanged genetically since its original introduction from tropical Africa (R.B. Clark, 1984, personal communication; Vinall et al., 1936). The response of Hegari to cultures that differed in Na/Ca ratio suggests that during its evolution as a crop species, Hegari may have been subjected to selection pressures in highly sodic soil environments, where the adaptive value of tolerance to high Na/Ca might be critical to survival. This tolerance appears to be associated with its greater ability to transport adequate Ca to the shoot meristem. Long distance transport of Ca seems to be correlated with transpiration rates that probably favor the more actively transpiring mature leaves (Marschner, 1986). However, the distribution of Ca between mature and immature blades of Hegari, unlike NK 265, for example, suggests that Ca is diverted from the older transpiring leaves and delivered preferentially to the younger blades. This may be because the young developing tissue provides a greater sink for Ca than do the transpiring leaves as Clarkson (1984) suggests in his exchange-site unloading theory. The extraordinary efficiency of Hegari to tolerate nutrient cultures low in available Ca may also explain its sensitivity to high external Ca concentrations, which reduced growth and caused severe chlorosis of older leaves. This response may be attributed to Ca/Mg imbalances in the shoots. In corn blades, increased Ca in concert with decreased Mg reduces photosynthetic activity by deterioration of chlorophyll (Peaslee and Moss, 1966). Furthermore, Ca directly inhibits the function of Mg requiring stroma enzymes such as fructose-1, 6-bisphosphatase, and alkaline pyrophosphatase (Brand and Becker, 1984).

In summary, the results of this study show that, under salt stress, sorghum genotypes differ greatly in their response to the Na/Ca composition of the root medium. At high external Na, Ca nutrition was affected and the genotypes differed in their ability to acquire, translocate, and distribute Ca efficiently. These important differences could be used to develop sorghum genotypes that would be adaptable to sodic soil conditions.

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