J. Plant Physiol. Vol. 137. pp. 64–71 (1990)

Physiological Basis of Differences in Salinity Tolerance of Pigeonpea and its Related Wild Species*

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Received April 30, 1990 · Accepted June 20, 1990

Summary

The physiological responses of a tolerant (ICPL 227) and a sensitive (HY 3C) cultivated pigeonpea [*Cajanus cajan* (L.) Millsp.] genotype and of tolerant (*Atylosia albicans, A. platycarpa* and *A. sericea*) and sensitive (*Rynchosia albiflora, Dunbaria ferruginea, A. goensis* and *A. acutifolia*) wild relatives were examined over a range of salinity levels. Transpiration rate decreased with increasing salinity in tolerant and sensitive pigeonpea genotypes and there were no consistent differences between them in this respect. Although leaf proline concentrations increased under salinity in the cultivated pigeonpea and in some of the wild relatives, there was no relation between salinity tolerance and proline accumulation. The greater salinity tolerance of *A. albicans, A. platycarpa* and *A. sericea* was associated with efficient sodium and chloride regulation in the plant system. Shoot sodium concentrations of the tolerant wild species were five to ten times less than those of the sensitive species, while root sodium concentrations in the tolerant species were two to three times higher than in the sensitive species. The potassium concentrations in the tolerant species increased with salinity, while in the sensitive species they decreased. Leaf magnesium concentrations remained unaffected with increasing salinity in the tolerant species, while in most of the sensitive species they decreased. Thus efficiency of regulation of ion transport to shoots seems to explain the differences in salinity response among pigeonpea genotypes and related wild species.

Key words: Cajanus cajan, ionic relations, physiological mechanisms, salinity tolerance.

Introduction

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is an important grain legume of semi-arid regions where salinity problems can be severe (Chauhan, 1987). Our initial evaluation of pigeonpea germplasm did not show a wide range of variation for salinity tolerance, as critical levels were confined to electrical conductivities of between 6 and 7 dS m^{-1} (Subbarao, 1988). However, a wide range of variation in salinity tolerance (from 4 dS m^{-1} to 12 dS m^{-1}) was observed among 15 wild relatives of pigeonpea belonging to the genera *Atylosia, Dunbaria,* and *Rynchosia* (Subbarao, 1988). *A. platycarpa* and *A. albicans* were identified as the most tolerant, being able to grow up to 12 dS m^{-1}, as compared with the most tolerant cultivated pigeonpea genotype, ICPL 227, which could tolerate salinity only up to 8 dS m^{-1} (Subbarao, 1988).

Salinity tolerance is generally considered a complex trait (Ramage, 1980; Woolhouse, 1981). This view may result from a lack of coordinated physiological and genetic research (Tal, 1985). Thus, genetic and physiological approaches should merge into a more comprehensive approach to breeding for salinity tolerance (Blum, 1988). An understanding of the physiological mechanisms and identification of the specific physiological traits conferring salinity tolerance could play a major role in the development of breeding strategies for transferring the higher level of salinity tolerance from wild relatives to cultivated pigeonpea. As a step in this direction, we examined the physiological behavior of cultivated pigeonpea genotypes and some wild relatives contrasting in their response to salinity.

* Submitted as JA No. 1028 by ICRISAT.

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Table 1: Relation between molar concentration and electrical conductivity of salinity treatments.

Molar concentration (mM)		Electrical conductivity (dS m^{-1})
NaCl	$CaCl_2$	
20	8	4
30	12	6
40	16	8
50	20	10

Materials and Methods

Experiment 1

Seeds of *Atylosia platycarpa, A. scarabaeoides, Rynchosia albiflora, Dunbaria ferruginea,* and pigeonpea genotypes ICPL 227 and HY 3C were obtained from ICRISAT's Genetic Resources Unit. Seeds of wild species require scarification to ensure germination. This was accomplished by nicking the testa with a scalpel. All seeds were surface sterilized with 0.2 % $HgCl_2$ solution for 5 min, then washed in several changes of deionized water. The seeds were germinated by rolling them up in blotting paper (15 × 10 cm) and placing the moistened «germination rolls» in plastic bags, which were incubated at 28 °C.

The growth medium consisted of sieved river sand. The sand was washed and soaked in acid solution (pH 1 to 2) for 24 h and then washed again with tap water. The dried sand was placed in 180 mm diameter polypropylene pots (2.5 kg sand pot^{-1}). Eight germinated seeds were sown per pot and the pots watered with deionized water until 13 days after sowing (DAS). The sand surface in each pot was covered with 50 g of polythene beads to minimize evaporation. On the 10th day, seedlings were thinned to four per pot. A modified Arnon and Hoagland nutrient solution (0.25 strength) with 1.79 mM NH_4NO_3 was used from 14 DAS. It was supplemented with NaCl + $CaCl_2$ (1 : 1 w/w) to give salinity treatments of 0, 4, 6, 8 and 10 dS m^{-1} (Table 1).

The composition of the nutrient solution in mM was: 0.23 KH_2PO_4, 0.52 KCl, 0.25 $MgSO_4$, 0.37 $CaCl_2$, 0.0015 $MnSO_4$, 0.00023 $ZnSO_4$, 0.00025 $CuSO_4$, 0.001 H_3BO_3, 0.00005 Na_2MoO_4 and 0.04 NaFeEDTA. At 14 DAS, the initial salinity level of 4 dS m^{-1} was imposed by flushing each pot with 1000 mL of 4 dS m^{-1} solution. For 6 dS m^{-1} and higher salinity treatments, the initial salt level of 4 dS m^{-1} was increased by 2 dS m^{-1} per day in the corresponding treatments so as to minimize salt shock to the seedlings. For the control (0 salinity) treatment only nutrient solution (ECe = 0.36 dS m^{-1}) was used. At the end of every day the evapo-transpirational losses were compensated for with deionized water. Pots were flushed with treatment solutions (250 mL pot^{-1}) on every 4th day to avoid salt accumulation. The pots were arranged in a complete randomized block design with the treatments replicated four times. The position of each pot was changed every 4 days, keeping the randomized design, to minimize spatial effects in the greenhouse, where the temperatures were 28/22 °C (day/night) and relative humidity was 60–70 % (mean day + night). Plants were harvested at 55 DAS.

At harvest, leaf area was measured with an automatic leaf area meter (Delta-T Devices Limited, U.K.). Fallen leaves were collected and included for dry weight determination and chemical analysis. Roots were carefully removed from pots and cleaned of sand by washing in water. Plant tops and roots were dried at 70 °C for 48 h and weighed. Plant samples were finely ground by a cyclone mill (UDY Corporation, Colorado, USA). For determination of element composition, finely ground samples of 200–300 mg were digested with 6 mL of a mixture of nitric, sulphuric, and perchloric acids (10 : 0.5 : 2) in a sand bath at 250 °C for 6–8 h (Piper, 1952). The digested plant samples were diluted and analyzed for various elements by atomic absorption spectrophotometry (Varian, 1200). Chloride content in plant samples was determined by Mohr's volumetric method (Blaedel and Meloche, 1960).

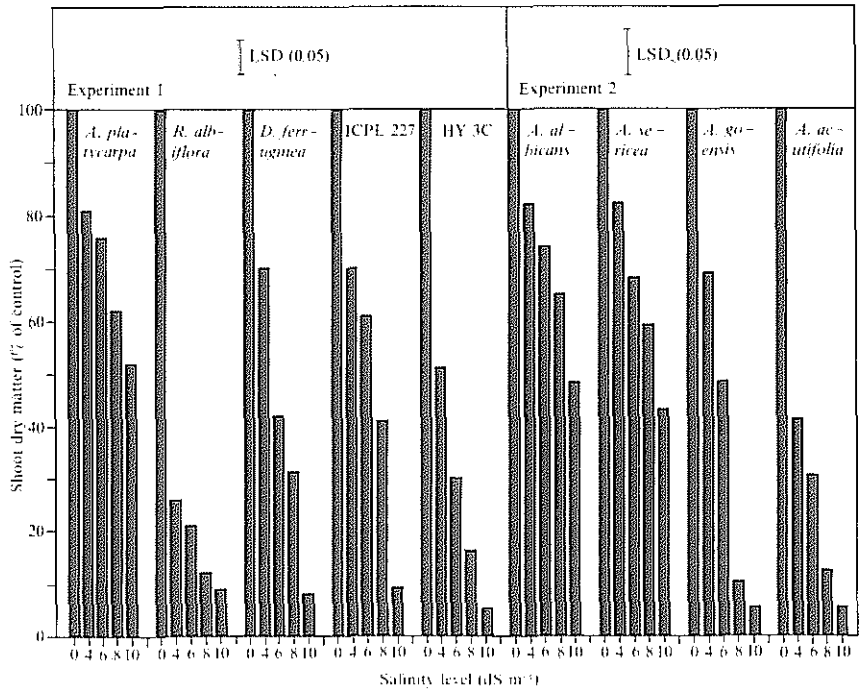

Fig. 1: Effect of salinity on relative shoot dry matter production of pigeonpea genotypes and related wild species.

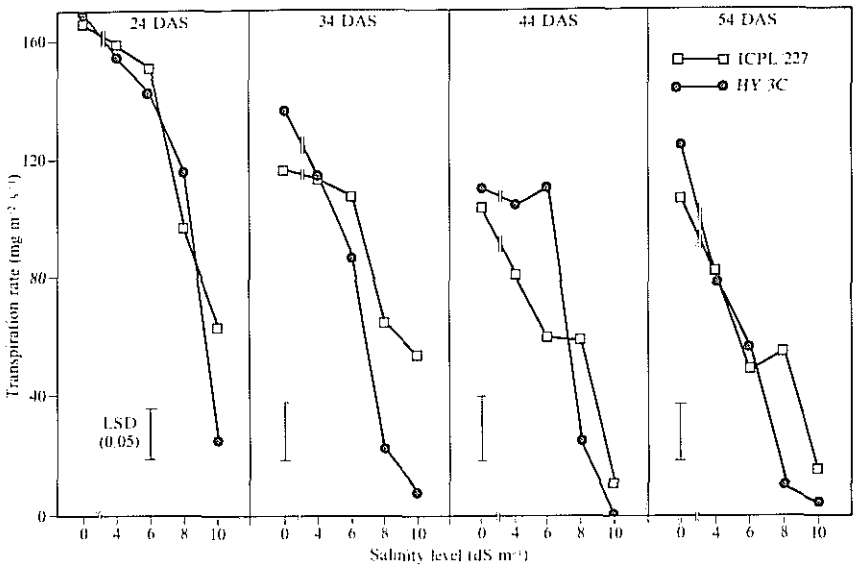

Fig. 2: Effect of salinity on transpiration rate of pigeonpea genotypes (Experiment 3). DAS = days after sowing.

Experiment 2

Ten species of *Atylosia, A. albicans, A. reticulata, A. acutifolia, A. cajanifolia, A. goensis, A. grandifolia, A. lineata, A. lanceolata, A. sericea* and *A. volubilis,* were grown for 55 days at salinity levels of 0, 4, 6, 8 and 10 dS m^{-1}. A randomized block design with treatments replicated four times was used. At 50 DAS, the first fully expanded trifoliate leaves were collected in zip polythene bags and stored at −11 °C for proline determination (Bates, 1973). The other experimental details and conditions were similar to those of Experiment 1.

Experiment 3

Pigeonpea genotypes ICPL 227 and HY 3C were grown for 75 days at salinity levels of 0, 4, 6, 8 and 10 dS m^{-1} under similar experimental conditions as described above. Stomatal conductance of the first fully expanded trifoliate leaves was recorded between 1100 h and 1200 h at 10-day intervals using a Steady State Porometer (LICOR Inc, LI 1600). At 30 and 45 DAS, the first fully expanded trifoliate leaves were sampled for proline determination.

Results and Discussion

Complete growth responses to salinity of pigeonpea genotypes and related wild species used in the present studies are being published separately (Subbarao et al., submitted). Here we examine the physiological behavior of cultivated pigeonpea genotypes and some wild relatives that differ widely in their tolerance to salinity: viz., in decreasing order of tolerance, *A. platycarpa* > *D. ferruginea* > *R. albiflora;* ICPL 227 > HY 3C; *A. albicans* and *A. sericea* > *A. goensis* and *A. acutifolia* (Fig. 1).

The transpiration rate decreased with increasing salinity in pigeonpea genotypes ICPL 227 and HY 3C (Fig. 2), as has been observed in many of the salt sensitive species (e.g., Gale et al., 1967; Longstreth and Nobel, 1979). Transpiration was reduced to a greater extent in HY 3C only at high salinity levels at the earliest samplings. Reduction in transpiration rate can also affect photosynthesis (Seeman and Critchley, 1985); hence this could possibly be one of the factors causing reduction of growth of pigeonpea under saline conditions.

Free proline concentrations in leaves of both pigeonpea genotypes and in one of the wild relatives increased under salinity (Fig. 3). At 10 dS m^{-1}, pigeonpea genotypes showed severe leaf burning symptoms and were on the verge of dying. No clear trends were apparent between the level of proline accumulation and the level of salinity tolerance in ICPL 227 and HY 3C. In one of the tolerant wild species, *A. sericea,* there was a 70-fold increase in leaf proline concentration at 10 dS m^{-1}, whereas in the other tolerant species, *A. albicans,* there was no accumulation of proline up to 10 dS m^{-1} (Fig. 3 b). In two of the sensitive species, *A. goensis* and *A. acutifolia,* there was a slight increase in leaf proline under salinity. It is generally found that various organic solutes (glycine betaine, proline, sucrose, sorbitol, mannitol and pinnitol) increase at high salinity levels in many species (Gauch and Eaton, 1942; Bernstein and Ayers, 1953) and have been considered to contribute to osmotic balance (Stewart and Lee, 1974), enzyme protection (Pollard and Wyn Jones, 1979) or perform other protective roles under saline conditions (Greenway and Munns, 1980). However, from the limited data of the present study, there appears to be no relationship between proline accumulation and response to salinity for pigeonpea and its wild relatives.

In all the species, shoot (leaf and stem) sodium concentrations increased with salinity (Fig. 4). However, the shoot sodium concentrations in the tolerant species (*A. platycarpa, A. albicans* and *A. sericea*) were about five to ten times less than in the sensitive species (*R. albiflora, D. ferruginea, A. acutifolia* and *A. goensis*). This was particularly so at 8 and 10 dS m^{-1}, levels at which these sensitive species failed to survive. Similarly, shoot sodium concentrations in ICPL 227 (tolerant) were about eight-fold less than in HY 3C at 8 dS m^{-1}. HY 3C perished at this level of salinity. Root sodium concentrations also increased under salinity in all the species. In *D. ferruginea, R. albiflora, A. goensis, A. acutifolia* and HY 3C, the root sodium concentrations increased up to

Fig. 3 a

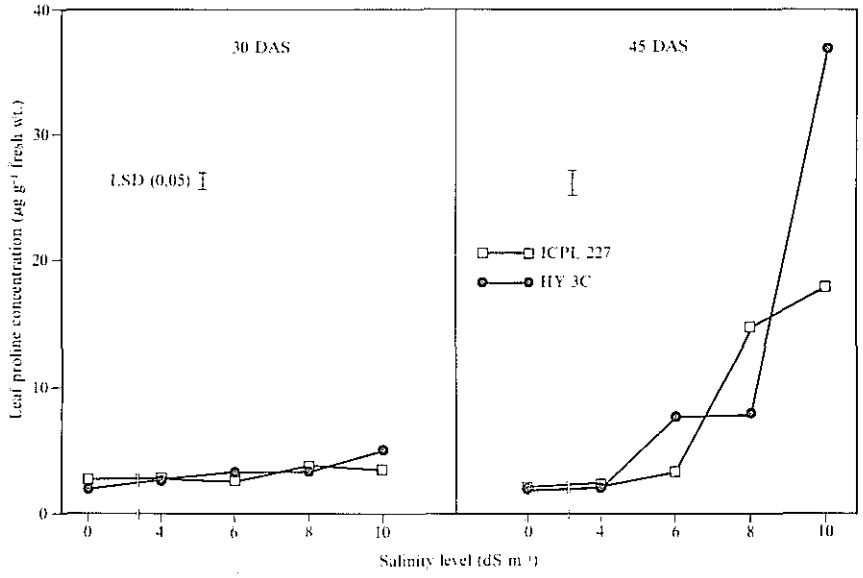

Fig. 3 b

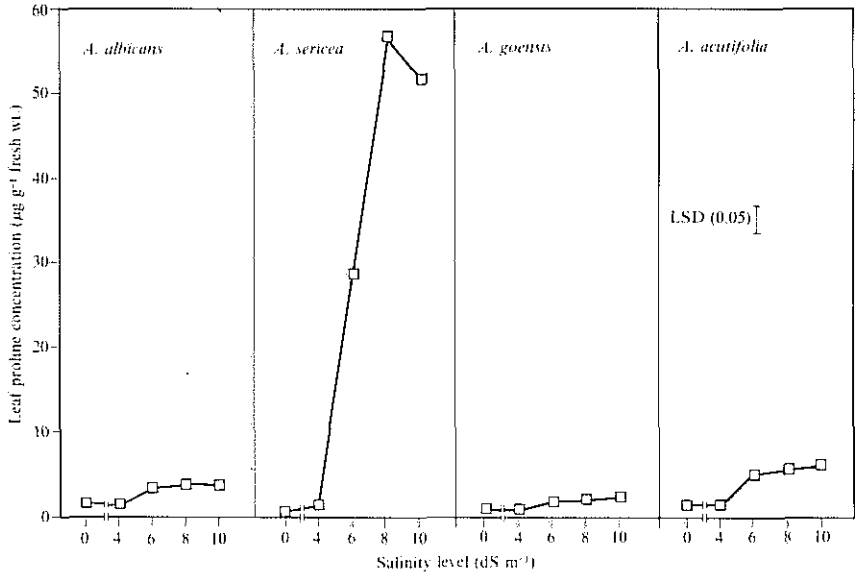

Fig. 3: Effect of salinity on leaf free proline accumulation in pigeonpea (Fig. 3 a – Experiment 3) and its related wild species (Fig. 3 b – Experiment 2).

6 dS m^{-1}, while there was a decline at 8 and 10 dS m^{-1}. In *A. platycarpa*, *A. albicans* and *A. sericea*, the root sodium concentrations continued to increase up to 10 dS m^{-1} and were about two to three times higher than in the sensitive species. It may be noted that, in many of the sensitive species, the decline in the root sodium concentrations at 8 and 10 dS m^{-1} was accompanied by a large increase in the shoot sodium concentrations.

Regulation of sodium movement into the plant system, particularly retention in the root and restriction of sodium translocation to the shoot, appears to be playing an important role in the salinity tolerance of wild relatives of pigeonpea. The same explanation holds for the differences in relative tolerance of ICPL 227 and HY 3C, where the sodium regulation ability is lost at 8 dS m^{-1} in HY 3C (sensitive) and at 10 dS m^{-1} in ICPL 227 (tolerant), resulting in a massive influx of sodium into the shoot system. Most of the legumes so far studied respond to saline conditions by exclusion of sodium and chloride ions from the leaves (Läuchli, 1984). There are also several other reports of tolerance being associated with exclusion of sodium and chloride from the shoot (e.g., Greenway, 1965; Läuchli and Wieneke, 1979; Gorham et al., 1986). This efficient sodium regulation in *A. platycarpa*, *A. albicans* and *A. sericea* may involve a series of physiological processes including: (a) effective regulation of sodium influx through efficient K/Na selectivity at the plasmalemma, (b) high retention of sodium in the root, and (c) sodium reabsorption from the xylem sap by the xylem parenchyma transfer cells during upward transport. The last one occurs in many species, particularly in legumes (Jacoby, 1965; Yeo et al., 1977; Läuchli and Wieneke, 1979).

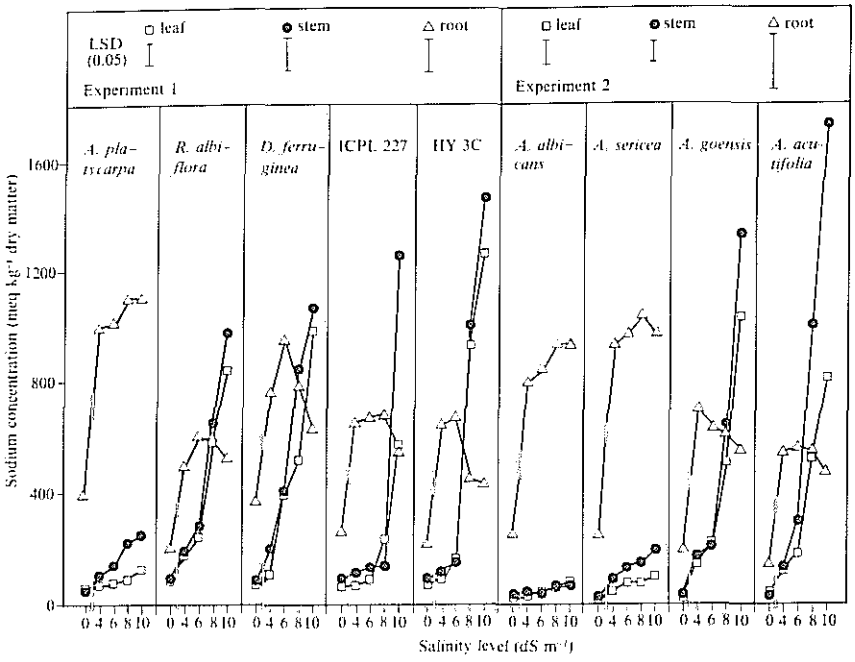

Fig. 4: Effect of salinity on tissue sodium concentrations of pigeonpea and its related *wild species*.

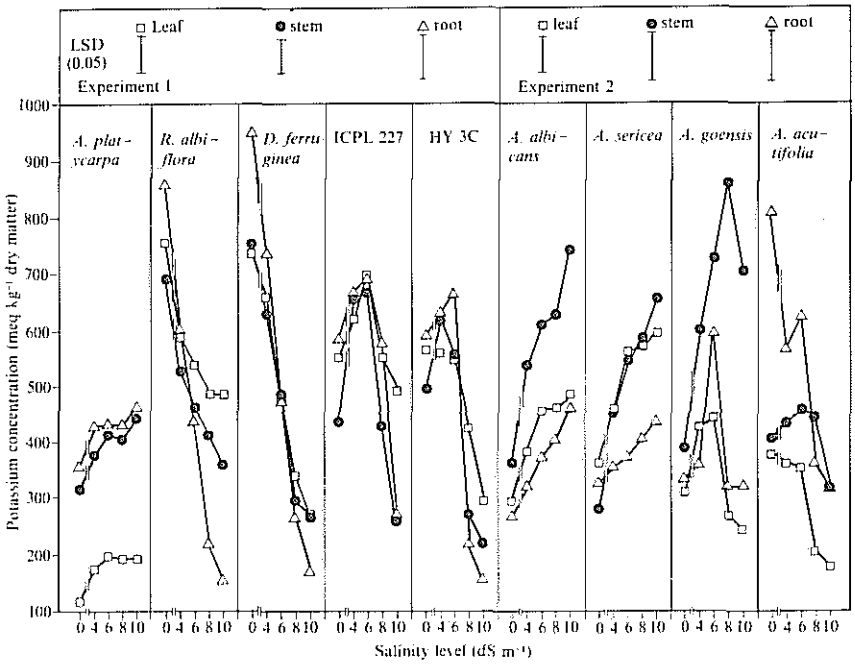

Fig. 5: Effect of salinity on tissue potassium concentrations of pigeonpea and its related *wild species*.

Retention of high concentrations of sodium in the root system (as in the tolerant wild species of pigeonpea), without disturbing the metabolism of root cells, is possible by efficient compartmentation of ions. Sodium must be excluded from the bulk of cytoplasm due to sensitivity of enzyme activity to high levels of sodium *in vitro* (Jennings, 1976; Flowers et al., 1977). It is still not clear up to what level of sodium is biochemically acceptable in the cytoplasm of different species of crops. In all of these tolerant species, the major increase in root sodium concentration occurred at 4 dS m^{-1}, and further increases are very small up to 10 dS m^{-1}. Also, there was no major increase in the shoot sodium concentration up to 10 dS m^{-1}. This indicates that even after the sodium retention capacity of the root is saturated, these tolerant species were able to regulate sodium inflow, synchronizing with expansion of retention capacity of the root (which is due to growth), without translocating to the shoot. The double requirement of salinity tolerance in protecting the cytoplasm against sodium and of maintaining osmotic balance could be met by a combination of an out-

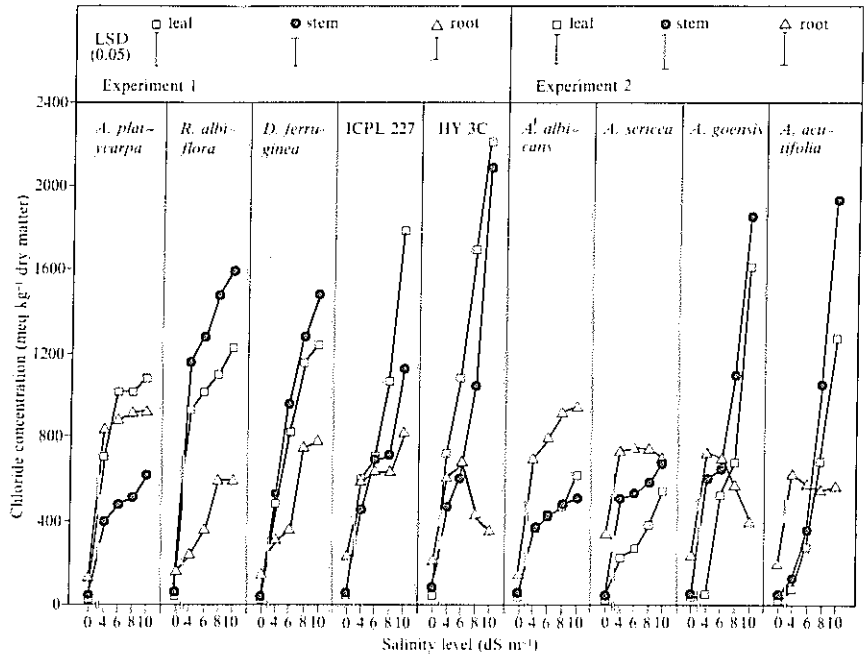

Fig. 6: Effect of salinity on tissue chloride concentrations of pigeonpea and its related species.

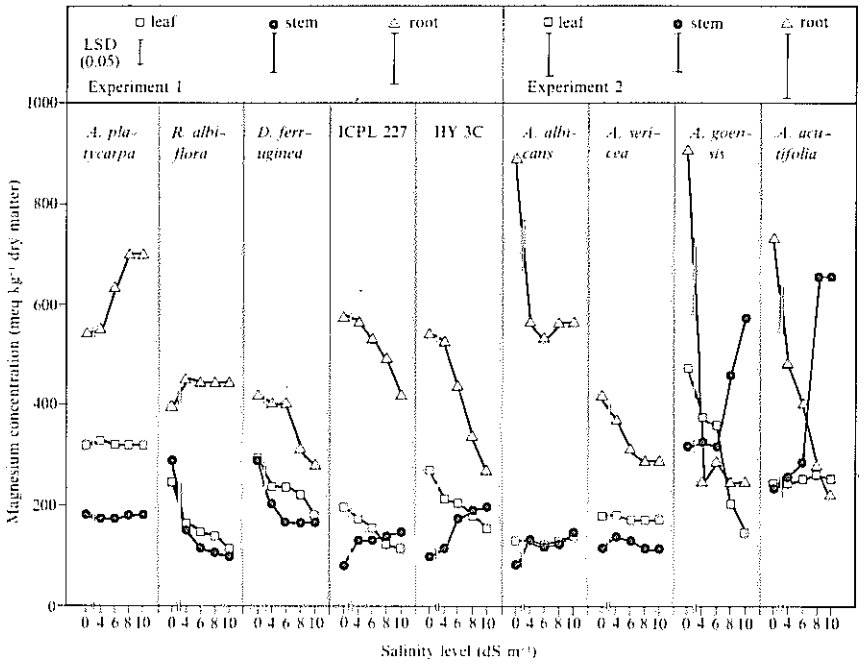

Fig. 7: Effect of salinity on tissue magnesium levels of pigeonpea and its related wild species.

wardly directed sodium pump at the plasmalemma and an inwardly directed pump at the tonoplast. This has been proposed for barley, where root cortex cells are able to sequester predominantly sodium into the vacuole while maintaining a high K/Na ratio in the cytoplasm (Jennings, 1968; Kylin and Hansson, 1971; Jeschke, 1980; Pitman et al., 1981). However, kinetic studies of ion fluxes and X-ray microanalysis would be required to confirm whether such mechanisms are applicable to pigeonpea.

Potassium concentrations in leaf, stem and root increased with increasing salinity up to 10 dS m^{-1} in *A. platycarpa*, *A. albicans* and *A. sericea* (Fig. 5). In ICPL 227, HY 3C, and *A. goensis*, potassium concentrations in the plant increased only up to 6 dS m^{-1}, and then declined at 8 and 10 dS m^{-1}. The potassium concentrations in ICPL 227 were significantly higher than in HY 3C, particularly at 8 dS m^{-1}. In *R. albiflora*, *D. ferruginea*, and *A. acutifolia*, potassium concentrations decreased with increasing salinity, showing the inabil-

ity of these species to maintain potassium selectivity under saline conditions.

Shoot chloride concentrations also increased with salinity in all the species (Fig. 6). In all the tolerant species, except *A. platycarpa*, the leaf and stem chloride concentrations were about two to three times less than in the sensitive species, particularly at 8 and 10 dS m^{-1}. *A. platycarpa* is an exception to this trend, where leaf chloride concentrations were high compared with the other tolerant species, but this species did not show leaf necrotic symptoms despite the high leaf chloride concentration (40 g kg^{-1} dry wt.). This indicates that the high chloride concentrations in the shoot are either tolerated in the cytoplasm or are compartmentalized within the leaf cells. Also, unlike sodium, chloride is usually considered biochemically inert and could be tolerated in the cytoplasm, acting as an important osmoticum (Clarkson and Hanson, 1980). However, very high concentrations of chloride in the shoot could disrupt metabolism and cause leaf necrosis and death (Greenway, 1965; Bernstein, 1975), as may have been the case in sensitive wild relatives and the cultivated pigeonpea.

Leaf magnesium concentrations remained relatively unaffected by increasing salinity in the tolerant species, while there was more than a 50% reduction in the sensitive species (Fig. 7). *A. acutifolia* was an exception to this trend. Root magnesium concentrations increased with salinity in *A. platycarpa* and *R. albiflora*, while in all the other species they decreased with increasing salinity. The concentrations of Mn, Zn and Fe in shoot and Ca in both shoot and root increased with salinity in all the species (data not presented) irrespective of their level of salinity tolerance. This suggests that uptake of these mineral nutrients would not be growth-limiting under saline conditions in pigeonpea and its related wild species.

The present study shows that the greater salinity tolerance of *A. albicans*, *A. platycarpa* and *A. sericea* is associated with their efficient regulation of sodium and chloride ions and maintenance of potassium selectivity under saline conditions. Further studies have shown that these physiological traits for *A. albicans* are expressed in the F_1 hybrids (reciprocal crosses) of *A. albicans* × *Cajanus cajan* (ICP 3783) (Subbarao, 1988).

Thus in pigeonpea and its related wild species, salt tolerance is a product of several possible physiological processes that govern sodium and chloride regulation and potassium selectivity. In any biological system, physiological processes involve a number of «steps»; each step in turn may be linked with a «trait». A breakdown at any one «step» may lead to a collapse of the whole system. Such a possibility receives support from the hypothesis of Shannon (1985) that «salinity tolerance STE 1 is probably the expression of a number of genes and the importance of each is dependent upon its interaction with the other salinity tolerance genes and the external salt concentrations».

Acknowledgements

We are indebted to Drs. D. L. Oswalt and F. B. Lopez, ICRISAT, for their critical comments on this manuscript.

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