Salinity Tolerance in Pigeonpea [*Cajanus cajan* (L.) Millsp] and its Wild Relatives

By

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C E R T I F I C A T E

This is to certify that the thesis entitled "**Salinity Tolerance in Pigeonpea [Cajanus cajan (L.) Millsp] and its Wild Relatives**" being submitted by Shri G.V. Subbarao for the award of the degree of **Doctor of Philosophy** of the Indian Institute of Technology, Kharagpur is a record of bonafide research work carried out by him under our supervision and guidance for about 4 years. The thesis is, in our opinion, worthy of consideration, for the award of the degree in accordance with the regulations of the Institute. The results embodied in the thesis have not been submitted to any other University or Institute for the award of any degree or diploma.

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1. INTRODUCTION

World crop production is limited largely by environmental stresses. Dudal (1976) estimated that only 10% of the world's arable land may be categorized as free of stress. However, statistics on the extent and impact of environmental stresses on crop production varies with the source.

Many of the high yielding varieties that contributed to production increases over the past few decades were deliberately developed to maximize yield under favourable environmental conditions. However, where it is not feasible to modify the environment to suit the plant, scientists are now being challenged to modify the plant to suit adverse environments while maintaining reasonable and reliable yields. In subsistence agriculture, which characterizes many third world countries, consistent performance under varying conditions is more important than high yield under favourable environments (Tal, 1985).

Salinity in arid and semi-arid regions of the world constitutes a major detrimental factor for crop production (Epstein, 1978). There are 344 million hectares of saline soils on the earth's land surface (Massoud, 1974) and, of these, 230 million hectares are not strongly saline and have crop production possibilities. The bulk of these soils are in arid and semi-arid lands where actual and potential salinity problems are most severe. An estimated area equivalent to 33% of irrigated land is affected by salinity, primarily caused by inadequate drainage (Carter, 1975). Prospects for the future are even

more ominous. According to some estimates, 40,000 hectares of irrigated land on the Indian sub-continent are becoming useless for crop production each year on account of secondary salinization (Raheja, 1966). In many of the agricultural ecosystems, more salt is delivered to the soil each year from irrigation than is removed by drainage. The inevitable consequence is a gradual build up of salts in the soil (Pillsbury, 1972).

Previously, this problem was tackled by means of one of two possible strategies. Saline soils have been reclaimed, drainage systems have been installed to remove excess salts, soil amendments have been used and high quality water has been conveyed long distances for irrigation and leaching. In short, the approach has been to modify the environment to make it suitable for the growth of conventional, that is salt sensitive, crop plants. Reclamation and drainage projects are extremely expensive operations, and subject to the availability of energy and high quality water. In many of the developing countries, there are neither the financial, technical nor the managerial resources available for installing and operating huge reclamation and irrigation schemes.

Application of a genetic approach to salinity is an idea whose time has come. No longer can agricultural scientists, addressing the staggering world-wide and threatening spectre of salinity, deal with it exclusively in management terms, although these endeavours have been continuing and will remain to continue. It is essential that a genetic dimension be added to the traditional approach of reclamation, drainage and use of excess irrigation water to leach salts below the root zone (Epstein, 1978). It is known that there is no biological

incompatibility between plant life and even highly saline conditions as evidenced by halophytes. The logical task would be to combine within the same plant the economic utility of a crop with the salt tolerance that plants evidently are capable of possessing.

In crop species, there is genetic diversity with regard to many agronomically useful traits. Salinity tolerance can not be an exception. The world collections of important crops are the chief repositories of this genetic wealth. Of the various crops, legumes are unique in several ways, for example, the ability to fix nitrogen, but are generally considered to be not very salt tolerant (Maas and Hoffman, 1977). These types of conclusions are often perfunctory, and the fact remains that their potential has not been explored and exploited so far. Certain legumes like Acacia and Prosopis can show extreme tolerance to salinity which can grow even with sea-water (ECe 46.3 dS/m) (Felkar et al., 1981). Variation for salinity tolerance has been reported in legumes although genetic variation within a crop species has been reported only in few cases (Ashraf et al., 1987). Legumes present additional challenges in finding tolerance to salinity as compared to cereals or other non-legumes, as one must take in to account the plant as well as its symbiosis with Rhizobium.

Pigeonpea is one of the important grain legumes cultivated in the arid and semi-arid regions where salinity problems tend to be acute. Over 90% of the world's pigeonpea production comes from India where salinity problems are becoming severe. An extensive world collection of pigeonpea germplasm and its wild relatives are being maintained at ICRISAT Center, Patancheru, Andhra Pradesh, India. These sources may have genetic diversity for salinity tolerance as they do for many

other characters. This possibility has not been very well explored so far since there is little information available on the genetic variability for salinity tolerance in pigeonpea. Since improvement of crop species took place outside their native areas or under favourable conditions, their gene pools have become limited (Rick, 1982). In addition, there is a growing feeling that physiological traits that are likely to play a role in salinity tolerance may have been lost in the cultivated crop gene pools over hundreds of years of domestication under favourable environments (Mudie, 1974; Maas and Nieman, 1978). Since wild relatives of the crop species were not passed through such selection pressure, the chances of obtaining high levels of tolerance to salinity may be good.

Although, introduction of genes from the wild salt tolerant species can be used to enrich crop species gene pools (Tal, 1985), the information on the genetic variability for salt tolerance in wild species that can be hybridized to crop plants is very limited (Epstein, 1978). In pigeonpea, slightly over 270 accessions of wild relatives of pigeonpea belonging to genera Atylosia, Rynchosia, Dunbaria, Paracalyx, Eracalyx, Eriosoma and Flemingia are available in the ICRISAT germplasm bank (Remanandan et al., 1988). Most of these wild types are compatible with the cultivated pigeonpea but there is no information about their salinity tolerance.

Genetic basis of many of the environmental stresses (salt, drought and others) are still considered as 'complex traits' (Ramage, 1980; Woolhouse, 1981). Much of the complexity stems from the lack of knowledge about the physiological mechanisms conferring tolerance and one of the important ways would be to resort to co-ordinated

physiological genetic research (Tal, 1985). Identification of specific physiological traits that play a major role in the tolerance mechanisms and establishment of their genetic basis is very crucial in the development of breeding strategies for the genetic improvement of crops to salinity tolerance. It is felt (Blum, 1988) that it is time to integrate plant physiology with plant genetic improvement towards a more comprehensive approach to breeding for environmental stress resistance in general, and salinity tolerance in particular.

Lastly, it is to be mentioned that the agricultural importance of legumes is particularly related to their ability to fix nitrogen in their root nodules. Any assessment of feasibility of growing legumes under saline conditions needs to consider the effects of salinity stress on legume-Rhizobium symbiosis. There is little information on the response of the pigeonpea-Rhizobium symbiotic system to salinity stress.

The major objectives of this research work are:

a. to assess the exploitable genetic variation for salinity tolerance in pigeonpea and its wild relatives.

b. to identify specific physiological traits involved in salinity tolerance and to understand the physiological and genetic basis of these traits.

c. to study the response of the pigeonpea-Rhizobium symbiotic system to salinity stress and to ascertain the range of variability among rhizobial strains in their symbiotic ability under salinity.

2. REVIEW OF LITERATURE

2.1 Salinity tolerance in legumes

Crop salt tolerance can be defined as 'the ability of plants to survive and produce economic yields under adverse conditions caused by soil salinity'. Salt tolerance of agricultural crops is typically expressed in terms of the yield decrease associated with soil salinity increases or as relative crop yield on saline vs. non-saline soils. A yield decrease of 50% is usually considered as the cutoff point for evaluating the relative salt tolerance of crops (ECe 50%) (Maas and Hoffman, 1977).

Legumes have long been recognized to be either sensitive or only moderately tolerant to salinity (Mass and Hoffman, 1977). However, considerable variability in salinity tolerance among crop legumes has been reported (Table 2.1). Among cultivated legumes, Sesbania cannabina is most tolerant (Keating and Fisher, 1985) (Table 2.1) and can tolerate and grow at salinity levels of 13.2 dS/m (ECe 50%), while Cicer arietinum is the most sensitive among legumes with tolerance only up to 3.0 dS/m (ECe 50%) salinity level.

Crop sensitivity to salinity stress varies depending on the growth stage. In Arachis hypogaea, salt tolerance was greater during germination than during subsequent growth (Shalhevet et al., 1969), whereas in lentil (Lens esculentum) it was found that germination was more sensitive compared to seedling growth stage (Jana, 1979). Salinity may stimulate the growth in some species. In Lupinus luteus,

'able 2.1 Relative tolerance of different legumes to salinity

Sl. No.	Species	ECe at 50% yield	References
1.	Sesbania cannabina	13.2	Keating and Fisher, 1985
2.	Lens esculenta	12.8	Rai, 1983
3.	Trifolium subterraneum	11.1	Hopmans et al., 1984
4.	Macroptilium atropurpureum	10.6	Keating et al., 1986
5.	Cyanopsis tetragonoloba	10.1	Keating and Fisher, 1985
6.	Medicago sativa	10.2	Russel, 1976
7.	Pisum sativum	10.0	Cerda et al., 1982
8.	Macroptilium atropurpureum	9.9	Russel, 1976
9.	Vigna triloba	9.7	Keating et al., 1986
10.	Indigofera spicata	9.5	Keating et al., 1986
11.	Macroptilium lathyroides	9.5	Russel, 1976
12.	Desmanthus subulatus	9.3	Keating et al., 1986
13.	Vigna sinensis	9.0	Keating and Fisher, 1985
14.	Sesbania bipinosa	8.4	Giridhar, 1987
15.	Trifolium alexandrinum	8.3	Russel, 1976
16.	Vigna aureus	8.3	Balasubramanian and Sinha,
17.	Medicago scutillata	8.2	Russell, 1976
18.	Trifolium hirtum	8.1	Russell, 1976
19.	Desmodium intortum	7.9	Russell, 1976
20.	Arachis pintae	7.9	Keating et al., 1986
21.	Macrotyloma uniflorum	7.8	Russell, 1976
22.	Medicago truncatula	7.8	Russell, 1976
23.	Medicago littoralis	7.7	Russell, 1976
24.	Vigna unguiculata	7.2	Russell, 1976
25.	Glycine wightii	6.9	Russell, 1976
26.	Vicia faba	6.8	Mass and Hoffman, 1977
27.	Glycine max	6.7	Keating and Fisher, 1985
28.	Lotononis bainesii	6.6	Russell, 1976
29.	Trifolium fragiferum	6.5	Russell, 1976
30.	Cliteria turnatea	6.4	Keating et al., 1986
31.	Trifolium repens	6.2	Russell, 1976
32.	Stylosanthus scaraba	5.6	Keating et al., 1986
33.	Lablab purpureus	5.5	Russell, 1976
34.	Cajanus cajan	5.4	Keating and Fisher, 1985
35.	Indigofera schimperi	5.4	Keating et al., 1986
36.	Psolarea tenax	5.3	Keating et al., 1986
37.	Rynchosia minima	5.1	Keating et al., 1986
38.	Stylosanthes humilis	5.1	Russell, 1976
39.	Vigna mungo	5.0	Keating and Fisher, 1985
40.	Arachis hypogaea	4.9	Mass and Hoffman, 1977
41.	Desmodium uncinatum	4.9	Russell, 1976
42.	Vigna unguiculata	4.9	Mass and Hoffman, 1977
43.	Trifolium semipilosum	4.2	Russell, 1976
44.	Phaseolus vulgaris	3.6	Mass and Hoffman, 1977
45.	Vigna radiata	3.5	Keating and Fisher, 1985
46.	Cicer arietinum	3.0	Saxena, 1987

there was a 50% fresh weight stimulation (over its control) at 50 mM NaCl (5 dS/m) salinity level (Steveninck et al., 1982).

Varietal or genotypic differences in salt tolerance have been reported in several legume crops (Table 2.2).

Table 2.2 Legumes where varietal or genotypic differences have been reported

Crop	References
Lentil	Jana, 1979; Rai, 1983
Alfalfa	Brown and Hayward, 1956
Pea	Cerda et al., 1982
Pigeonpea	Paliwal and Maliwal, 1973; Gururajarao et al., 1981;
Chickpea	Lauter and Munns, 1986; Saxena, 1987; Goel and Varshney, 1987
Subterranean clover	West and Taylor, 1981
Cowpea	Paliwal and Maliwal, 1973
Soybean	Wieneke and Lauchli, 1979
Berseem clover	Ashraf et al., 1987
Red clover	Ashraf et al., 1987

For a few crops, variation to salinity tolerance within a variety has been reported. In Medicago sativa, large variation in salt tolerance within the variety CUF 101 was reported (Noble et al., 1984). In Trifolium alexandrinum (Ashraf et al., 1987), and T. pratense (Ashraf et al., 1987) similar variation has been reported.

The adverse effect of salinity was attributed to specific ion toxicity. In lentil, germination and growth were severely inhibited by MgSO4, followed by MgCl2 (Jana, 1979), while in chickpea was less affected by Na2SO4 salinity than NaCl salinity (Lauter and Munns, 1986).

Climatic factors may significantly influence plant response to salinity, with temperature and atmospheric humidity being most important. Many crops behave less salt tolerant when grown under hot-dry conditions than under cool humid conditions. Relative yields of alfalfa and bean were more depressed in warm than in cool climates (Magistad et al., 1943). A similar response was seen in alfalfa and clover (Ahi and Powers, 1938). The salinity tolerance of bean grown in a cool climate is significantly higher than when grown under hot conditions (Hoffman and Rawlins, 1970). High atmospheric humidity increased the salinity tolerance in beans (Hoffman and Rawlens, 1970).

2.2 General response of plants to salinity

Levitt (1972) classifies the adverse effects of salts on plants into three categories which included (a). osmotic stress, (b). specific ion effects, and (c). nutritional deficiency.

If salt stress lowers the external water potential below that of the cell, it exposes the cell to a secondary water deficit stress. To distinguish this from salt stress, and because it leads to osmotic dehydration, it is called osmotic stress (Levitt, 1972). It has also been called 'physiological drought'. In the absense of specific ionic effects, crop growth reduction due to salinity is generally related to the osmotic potential of the root zone soil solution (Bernstein, 1975; Maas and Hoffman, 1977). Osmotic potentials can be related to the electrical conductivity (dS/m) of extracts from saturated soils by the formula $\psi_o = -0.36$ ECe. Decreasing osmotic potential in the root zone soil has the net effect of reducing the availability of water to plants. Therefore, plants growing on saline soils often appear to be

suffering from drought.

An excess of specific ions may be toxic to various plant physiological processes including nutritional disorders. Ions contributing appreciably to specific ion effects include Cl, SO4, HCO3, Na, Ca, Mg. In combination, these ions may contribute to osmotic effects. Polyethylene glycol (PEG) permitted large yields from bean plants compared to yields obtained in iso-osmotic solutions containing Na, Ca, and Mg chlorides (Lagerwerff and Eagle, 1961). At equal osmotic concentrations, NaCl depresses the germination of alfalfa seeds much more than does mannitol (Strogonov, 1964).

The possible effects of specific ions are not well understood (Levitt, 1972). Specific ions may influence respiration as found in pea roots (Porath and Poljakoff-Mayber, 1964). It was recorded that NaCl, CaCl2 and Na2SO4 inhibited the production of chlorophyll and carotene in grape fruit tree leaves (Carter and Myers, 1963). High sodium can cause calcium and magnesium nutritional deficiencies (Geraldson, 1957). Sodium chloride salinity induced various changes in the anatomy of the plants (Strogonov, 1964).

There have been many reports of salt induced decreases in several metabolic processes such as respiration (Boyer, 1965; Siew and Klein, 1968), photosynthesis (Gale et al., 1967; Deshpande and Nimbalkar, 1982; Gilmour et al., 1985), protein synthesis (Rakova et al., 1969; Shevyakova and Komizerki, 1969;), and nucleic acid synthesis (Rauser and Hanson, 1966). Strogonov (1964) singled out the nitrogen metabolism as the source of the injury. The salt induced growth retardation leads to an accumulation of unused substances

(Gauch and Eaton, 1942). The changes in nitrogen metabolism are usually accompanied by the accumulation of ammonia, amines, diamines (putrescene, cadavarine), amino acids (hydroxyproline, proline, leucine, isoleucine, alanine, phenylalinine and tyrosine) which can have an adverse effect on the physiological processes of the plant (Strogonov, 1964). The actual toxic substances vary from species to species, depending on the metabolism of each species. Reports have shown that potassium deficiency also leads to an accumulation of putrescene (Smith, 1965; Crocomo and Basso, 1974). If excess sodium interferes with potassium absorption, it would lead to the accumulation of putrescene for the same reason. Munns et al. (1983) however warned that most of the existing data on the metabolism of plants under stress conditions described the consequences rather than the causes of reduced growth.

2.3 Mechanisms of salinity tolerance

In saline environments, the adverse effects of low external water potential can be remedied by uptake of electrolytes (Na, Cl), but this uptake also creates the danger of 'ion excess' where high internal ion concentrations reduce growth'. In this potentially disastrous situation, different species may develop diverse mechanisms of adaptation (Greenway and Munns, 1980).

Halophytes rely mainly on ions (Na, Cl) for turgor maintenance, a response similar to that of highly vacuolated marine algae (Cram, 1976). These halophytes generate turgor by high internal sodium and chloride concentrations. Current reviews by (Flowers et al., (1977) and Wyn-Jones et al., (1979) suggest that these high ion

levels can be tolerated because sodium and chloride concentrations are relatively low in the cytoplasm as compared with the vacuole, while neutral solutes like proline, glycine, betaine and sucrose contribute to the osmotic potential of cytoplasm. Additional adaptive features which contribute to the avoidance of high ion concentrations in the leaves of some species include salt glands and bladders (Jennings, 1976 ;Flowers et al., 1977).

In non-halophytes, it is difficult to assess the relative importance of ion excess and water deficit. Greenway and Munns (1980) suggested that non-halophytes are usually affected by either ion excess in the expanded leaves or by water deficits in the expanding leaves. There is evidence that in several species the salt sensitivity is due to 'ion excess' which is based on the relationships between internal ion concentrations and salt tolerance. High chloride concentrations in expanded leaves are associated with chlorosis and death (Bingham et al., 1968; Bernstein et al., 1969; Bernstein, 1975). Similar observations were made by Greenway (1965) in barley, where high chloride absorption correlated with appearance of chlorosis and the total chloride concentration.

Sensitivity towards high chloride and sodium in leaves is much greater for non-halophytes than for halophytes. Extreme halophytes such as Suaeda maritima can avoid adverse effects of chloride and sodium even when the concentrations reach 600 to 650 mM in the mesophyll (330 mM NaCl) (Flowers, 1972). In non-halophytes, growth is severely reduced when ion concentrations in the leaves are as low as 100 mM chloride (Greenway and Munns, 1980). In vitro studies have shown that soluble enzymes from halophytes and non-halophytes have

similar sensitivity to electrolytes (Flowers et al., 1977; Jennings, 1976). This confirms the hypothesis that in halophytes, the maintenance of lower concentrations of sodium and chloride in the cytoplasm compared to those in the vacuole, could be responsible for the ability to tolerate 600 mM sodium and chloride concentrations internally without any disturbance in the metabolism (Yeo, 1974).

2.3.1 Role of cytoplasmic organic solutes in salinity tolerance:

It has been suggested that high concentrations of organic solutes in the cytoplasm can contribute to the osmotic balance when electrolytes are lower in the cytoplasm than in the vacuole (Stewart and Lee, 1974). There can be a protective effect on enzymes in the presence of high electrolytes in the cytoplasm (Pollard and Wyn-Jones, 1979). Organic solutes which increase at high salinity in many species include glycinebetaine, proline (Storey and Wyn-Jones, 1977) and sucrose (Gauch and Eaton, 1942; Bernstein and Ayers, 1953). These compounds at concentrations up to 500 mM do not appreciably inhibit in vitro enzyme activity (Pollard and Wyn-Jones, 1979). Many amino acids and carbohydrates, at 0.1 to 1M, mitigated or prevented the loss of activity of several enzymes (in vitro) (Pollard and Wyn-Jones, 1979). Glycine betaine (500 mM) alleviated the inhibitory effects of 200 mM NaCl on malic enzyme isolated from barley (Pollard and Wyn-Jones, 1979). Greenway and Munns (1980) suggested that a wide range of solutes can perform similar protective or osmotic roles. This is illustrated by the report of substantial increases in sorbitol in Plantago maritima (0 to 400 mM NaCl), a species which accumulates neither proline nor glycine

betaine (Ahmad et al., 1979).

Greenway and Munns (1980) suggested that an adaptive role of proline is related to survival rather than to maintenance of growth. The hypothesis is that proline accumulates due to reduced turgor or reduced growth. In three halophytes, salt tolerant and sensitive species accumulated substantial quantities of proline (greater than 214 mol/g FW) only when growth is severely reduced and there is no evidence that proline accumulates more in salt tolerant than in salt sensitive species (Storey and Wyn-Jones, 1979) and it is likely that the reverse is true (Tal et al., 1979).

2.3.2 Regulation of Na and Cl concentrations in the shoot

In halophytes, inorganic ions (Na, Cl) are used for turgor maintenance through effective compartmentation into the vacuole (Flowers, et al., 1977), coupled with salt excreting mechanisms like salt glands or salt bladders in the shoot system which could effectively excrete the excess sodium and chloride that could not be compartmentalized in the shoot tissues and would effectively prevent 'ion excess'. Most non-halophytes are probably unable to synchronize compartmentalization of ions within individual leaf cells and have a high ion uptake into the leaves, leading to 'ion excess'. The key factor for the tolerance in the non-halophytes to salinity is a synchronization of ion compartmentalization by the leaf cells with a regulation of ion transport to the shoot (Greenway and Munns, 1980). In the absence of any salt excreting mechanisms and the limited compartmentalization ability of Na and Cl of the shoot system, the mechanisms that regulate the sodium and chloride transport to the

shoot play a major role in preventing the 'ion excess' in non-halophytes.

2.3.2.1 Regulation of sodium: The key control points in regulating sodium transport in the whole plant appear to be a series of membrane transport processes in root, stem, and leaves (Lauchli, 1984). The main barrier to passive sodium flow to the shoot is certainly the suberized endodermis, at this location nearly all the water has to be passed through cell membranes with a low permeability to sodium. Even so, if sodium concentrations in the xylem are as low as 1% of the external solution, the leaf sap would still increase by 40 to 70% for each increase of 100 mM NaCl (Munns et al., 1983). However, high concentrations in leaves could be prevented if ions were removed from the xylem during upward transport and this occurs for sodium in some salt sensitive species (Jacoby, 1965; Lauchli and Wieneke, 1979; Walker, 1986).

In barley roots, the cortex cells are able to sequester predominantly sodium in the vacuole while maintaining a high K/Na ratio in the cytoplasm (Jeschke, 1980; Pitman et al., 1981). This important pattern of ion compartmentation appears to be brought about by selective K influx and Na efflux at the plasmalemma and by Na/K exchange at the tonoplast (Jeschke, 1980), however the capacity of root cells for sodium sequestration in vacuoles under saline conditions is not clearly understood.

In legumes, sodium specific events in the vacuolar tissues of the proximal region of the root and the base of the stem are of primary significance (Jacoby, 1965). Following up on Jacoby's work, Kramer et al. (1977) revealed the existence of transfer cell like xylem parenchyma cells in the proximal region of the roots of Phaseolus coccineus, where sodium accumulated to levels greatly exceeding those in the apical root and the leaves. Using X-ray micro analysis, these authors further demonstrated very high Na/K ratios in the xylem parenchyma cells, in contrast to the xylem vessels where the ratio was approximately at unity. Chloride did not accumulate in the xylem parenchyma cells.

Lauchli (1976) concluded that sodium accumulation in the xylem parenchyma cells is due to sodium reabsorption from the xylem sap in exchange for potassium, possibly by a Na/K exchange process operating at the plasmalemma of these transfer cells. In view of the evidence given by Jeschke (1980), on Na/K exchange at the tonoplast of root cells, it is feasible that the tonoplast of the xylem parenchyma cells in bean roots is also important in sodium reabsorption from the xylem vessels and controls sodium accumulation in the vacuole of the xylem parenchyma cells. Whatever the mechanism of sodium reabsorption, this process contributes effectively to sodium exclusion from the leaves (Lauchli, 1984). Its practical importance for conferring salinity tolerance, may be limited to short duration of salinity stress because the capacity of the xylem parenchyma cells to accumulate sodium may become rapidly exhausted, as discussed by Luttge (1983).

Sodium retranslocation from the leaves could also contribute in maintaining low levels of sodium in the leaves (Lauchli, 1984). However, phloem loading of sodium in leaves may not be very significant since maintenance of low sodium concentrations in the root symplasm may also apply to sieve tubes, which are considered to form a symplasmic pathway (Pitman et al., 1981). Marschner and Ossenberg-Neuhas, (1976) reported significant sodium retranslocation through the phloem to the root followed by sodium efflux from the proximal root to the growth medium, but the sodium amounts applied and transported were low. Lessani and Marschner (1978) examined the significance of retranslocation of sodium for regulation of sodium concentration in the leaves and its relation to salt resistance in several species. They found that with 100 mM NaCl in the medium, there were significant correlations between decreases in dry matter production and sodium retranslocation from the leaves and in particular, efflux from the roots. Efflux from the roots increased with decreasing salinity tolerance. This shows that regulation of net sodium import to the leaves primarily controls sodium regulation or exclusion and salinity tolerance rather than retranslocation from the shoot to the root. Indirect support of this conclusion comes from the work by Winter (1980) and Winter and Presten (1982), who demonstrated that in the leaves of Trifolium alexandrinum grown at 50 mM NaCl, there was gradual destruction of the phloem transfer cells prior to the development of leaf burn due to salt toxicity (Winter, 1980). The destruction of phloem transfer cells coincided with high Na/K ratios in these cells (Winter and Preston, 1982). Thus the build up of sodium in the leaves probably caused the breakdown of sodium export through the phloem.

2.3.2.2 Chloride regulation: Salt tolerant soybean varieties maintained low levels of chloride in the shoot compared to susceptible varieties (Abel and Mackenzie, 1964). Lauchli and Wieneke (1979) studied ion distribution in the soybean varieties 'Lee' and 'Jackson' and suggested that chloride exclusion from the leaves of tolerant 'Lee' is regulated by the root. Wieneke and Lauchli (1979) showed that chloride influx into roots of 'Lee' over a wide range of salinity levels was much lower than in the salt sensitive non-excluding variety 'Jackson'. Furthermore 'Lee' transported considerable amounts of chloride to the shoot immediately upon the onset of the salinity treatment and then effectively controlled chloride transport to the shoot, contrary to the behaviour of 'Jackson'. X-ray microanalysis revealed that chloride accumulated in the cortex of the apical root of the cultivar 'Lee' suggesting that chloride accumulation in the root is mediated by sequestration of chloride in the vacuoles of the cortex (Lauchli and Wieneke, 1978).

Based on these findings, Lauchli (1984) proposed a model to explain the regulation of chloride transport in roots of soybean. It indicated that the low chloride flux to the xylem and the shoot of the tolerant cultivar was mainly a consequence of low root influx and high vacuolar transport. In contrast, the sensitive cultivar had high root influx coupled with inefficient vacuolar transport and thus the high flux to the xylem loading leads to uncontrolled chloride transport to the shoot and causes 'ion excess'. X-ray microanalysis data from Lupinus luteus (Steveninck et al., 1982) indicate that the apparent lack of chloride exclusion in this species was due to low rates of chloride accumulation in the vacuoles of the cortex cells. Lessani

and Marschner (1978) examined the significance of retranslocation of chloride from the shoot in regulation of chloride levels in the shoot, and its relation to salt resistance in several species. They found no correlation between the extent of chloride retranslocation and growth depression caused by salinity.

2.3.3 Responses of different genotypes:

High total electrolyte concentrations in the shoot, resulting from high rates of uptake, have often been considered as an essential adaptive feature of those halophytes which grow rapidly at high salinity (Flowers et al., 1977; Wyn-Jones and Storey, 1978). Comparisons between species with extreme differences in salt tolerance support the view that high electrolyte concentration in leaves is an adaptive trait. In a comparison of seven species, Lessani and Marschner (1978) reported that the highest chloride levels occurred in beans and in sugar beet (25 to 100 mM NaCl). Furthermore (Na+K) was very high in both salt sensitive pepper and salt tolerant sugarbeet at 0 mM as well as 100 mM NaCl in the external solution. The case for the adaptive value of high internal electrolyte concentrations is strengthened by comparisons between closely related species of tomato (Dehan and Tal, 1978). The wild species Lycopersicon cheesmani (Rush and Epstein, 1976) and Solanum pennellii (Dehan and Tal, 1978) had typical halophytic responses compared with the cultivated tomato (L. esculentum).

Leaves of salt tolerant varieties of certain non-halophytes such as Avocado (Downton, 1978), Glycine max (Lauchli and Wieneke, 1979) and Hordeum vulgare (Greenway, 1965) have 1.3 to ten-fold lower concentrations of Cl and sometimes sodium than sensitive varieties. Similarly in Festuca rubra, a wild monocotyledon, shoots of salt tolerant clones from saline marshes had two to three fold less Cl and Na than those of sensitive clones (Rozema et al., 1978). Better exclusion of chloride from the shoots of Casuarina equisetifolia (tolerant) than C. cunninghamiana (moderately tolerant) was due to a lower chloride uptake and lower net transport into the shoot rather than its retention in the roots or reabsorption at the proximal root or hypocotyl (Aswathappa and Bachelard, 1986).

Differences between salt resistant and salt sensitive species of Plantago were located in the ion secretory system which was involved in the ion translocation from the root to the shoot rather than in the primary uptake process through the plasmalemma of the cortical cells (Erdei and Kuiper, 1979). Many of the perennial Triticeae showed good salinity tolerance which was associated with the ability to exclude sodium and chloride and to maintain high leaf potassium levels (Gorham et al., 1986). The salinity tolerance in perennial Triticeae members such as Leymus sabulosus and Elytrigia juncia, was associated with an ability to tightly control osmotic adjustment by strictly regulating the influx of sodium and chloride. Thus salinity tolerance in these grasses implies strict control of tissue salt levels, not high exclusion of salt under all circumstances. A genetic basis was established for the large differences in chloride concentrations in leaves of soybeans (Abel, 1969) and for salt tolerance in Festuca

rubra (Venables and Wilkins, 1978).

Roots of salt tolerant grape vines contained only 15 to 25% of the Cl concentrations of sensitive varieties (Bernstein et al., 1969), but a tolerant soybean variety had about two fold higher Cl than a sensitive variety (Lauchli and Wieneke, 1979). Other studies with Hordeum vulgare (Greenway, 1965)and Glycine (Wilson et al., 1970) have shown no such large varietal differences in either root Cl or Na.

The association between high ion concentrations in leaves and salt sensitivity was by no means general. In rice (Oryza sativa) one tolerant variety did have low sodium in its leaves, but another tolerant variety had high sodium (Greenway and Munns, 1980). In other investigations, maize varieties which differed substantially in salt tolerance had similar ion concentrations in the leaves (Lessani and Marschner, 1978). Varietal differences in salt tolerance, despite similar ion concentrations in the shoots, may be related to differences in : a) tolerance to low external water potential, b) differences in ion compartmentation in the leaves, c) ion compartmentation in roots, d) ion compartmentation between leaves of different ages (Greenway and Munns, 1980).

2.4 Role of calcium in salinity tolerance

It has long been realized that plants grow better in saline conditions when calcium is present. Several studies reported that supplemental calcium may mitigate reduced growth due to NaCl salinity. Elzam and Epstein (1969) observed a strong correlation between growth and calcium levels in the root tissue while recording the effect of

increasing NaCl on the growth and salt content of two species of Agropyron. One species (A. elongatum) was salt tolerant, and could grow reasonably well at 50 mM NaCl, whereas the sensitive species (A. intermedium) suffered a severe growth reduction even at 5 mM NaCl. In Phaseolus vulgaris, dry weights increased with increasing calcium levels up to 3 mM at 50 mM NaCl salinity and there was no further improvement in growth afterwards (Lahaye and Epstein, 1969). Hyder and Greenway (1965) in studies with barley, attributed the higher growth under saline conditions mainly to the increased calcium status of the medium. In a recent study with rye grass (Lolium rigidum), Marcar (1986) showed that germination and seedling growth improved under NaCl and MgCl2 salinity with increasing calcium concentration in the medium.

The importance of calcium for selective ion uptake by plants is well documented (Epstein, 1961; Rains, 1972). Increasing the level of salts in the medium surrounding the roots of plants resulted in greater demands on the salt regulating processes of plants. The ratio between required ions (eg. K) and unessential ions (e.g Na) is reduced, with the unessential ions predominating in many saline systems. Selective ion transport then becomes paramount to survival. The presence of potential toxic ions (particularly Na) will increase the possibility of membrane damage. Gerard and Hinojosa (1973) observed in cotton that under low calcium levels in the medium (<1 mM) NaCl salinity reduced the calcium uptake and concentration in the roots. Low calcium has been considered to increase the membrane permeability leading to an increase in passive chloride and sodium transport responsible for 'ion excess' (Lahaye and Epstein, 1971). In

a recent study with corn root protoplasts, Cramer et al. (1987) observed a decrease in the membrane associated calcium content due to displacement of calcium by sodium, thus disrupting membrane integrity. NaCl salinity has been reported (Lynch and Lauchli, 1985) to disturb the calcium nutrition by inhibiting calcium transport from root to shoot in barley, by interferring with the release of calcium into the root xylem, possibly through an effect on the active loading of calcium into xylem vessels.

Calcium can minimize the leakage of cytosolic potassium, thus contributing to maintenance of the turgor (Cramer et al., 1985). Several studies point out that calcium plays an important role in the selective absorption of K (Rains and Epstein, 1967; Elzam and Epstein, 1969; Cramer et al., 1985; Kent and Lauchli, 1985) by restricting the entry and translocation of sodium (Lahaye and Epstein, 1971) and thereby increasing the K/Na ratio in the cytoplasm, essential for the normal metabolism of plants. Calcium could also play a role in the protection of the nitrate transport mechanism during saline conditions (Ward et al., 1986). It is not known whether this enhancement of nitrate uptake by calcium under saline conditions is due to improved uptake of potassium, since nitrate uptake and translocation are stimulated by potassium (Blevins et al., 1978; Frost et al., 1978). Calcium also modifies the permeability of cytoplasmic surfaces in such a way as to decrease the access of monovalent cations (particularly sodium) to the absorption sites, and also modifies the selectivity of the cell membrane for monovalent cations (Jacobson et al., 1960; Moore, 1960). Thus the role of calcium becomes even more important as the system becomes increasingly saline.

The ability of calcium to enhance the tolerance of Phaseolus vulgaris to sodium is reported to be a function of temperature. Ayoub (1974) showed that in cool seasons calcium caused competitive inhibition of sodium uptake and translocation while it had no beneficial effect in warm seasons. In rice, however, increasing calcium in the medium did not ameliorate the effects of NaCl salinity on growth. Yeo and Flowers (1985) concluded that rice roots weakly respond to calcium and that they are capable of better permeability control than was evoked by calcium ions. In lettuce, also there was no ameliorative effect of supplemental calcium on growth (Cramer and Spurr, 1986). Greenway and Munns (1980) suggested that responses of different species to high Na/Ca were related to differences in their membrane structure. However, it is intriguing that species which are most sensitive to very high Na/Ca per se are also most sensitive to high concentrations of soluble salts (Bower and Wadleigh, 1948; Eaton, 1942).

2.5 Symbiotic nitrogen fixation under salinity stress:

Nodule initiation in the legume-Rhizobium symbiosis involves a complex interaction between host root, rhizobial strain and the environment. Salinity stress may differently affect each phase of the legume-Rhizobium symbiosis: (a) rhizobial survival and growth in the rhizosphere of the host, (b) rhizobial infection of the host root hair, (c) nodule initiation and development, (d) nodule functioning (nitrogen fixation) and (e) growth of the host legume. Distinguishing which phase is primarily affected may not be easy due to the close interdependency of these phases.

salinity.

Total nitrogenase activity decreased with increasing salinity in Glycine max (Singleton and Bohlool, 1984), Trifolium subterraneum (Hopmans et al., 1984) and Vicia faba (Yousef and Sprent, 1983) while in Macroptilium atropurpureum and Neonotonia wightii, specific nitrogenase activity was not affected by increasing salinity (Wilson, 1985). In Pisum sativum, leghaemoglobin content decreased with the increasing salinity and brought about enhanced senescence of nodules (Siddique et al., 1985).

In Glycine wightii (Wilson, 1970) and Vicia faba (Yousef and Sprent, 1983) rhizobial inoculated plants were more affected with increasing salinity compared to the nitrogen-fed plants, which indicated that symbiotic sensitivity to salinity stress could be a limiting factor for growth in these species. Leaf nitrogen levels (%) decreased with increasing salinity in nodulated Glycine max (Singleton and Bohlool, 1984), Trifolium subterraneum (Hopmans et al., 1984), Pisum sativum (Siddique et al., 1985) and Vicia faba (Yousef and Sprent, 1983). This confirms that insufficient nitrogen could be fixed to meet the requirements of these legumes thus leading to nitrogen deficiency.

Significant interactions were reported in nitrogen fixation between rhizobial strains and genotypes of lentil under saline conditions (Rai, 1983), thereby indicating that rhizobial strains of a single species could vary in their symbiotic ability under saline conditions. Selection of rhizobial strains need not be confined to the strains collected from saline soils alone. In R. leguminosarum

and R. trifolii, there were no differences between rhizobial strains collected from saline and non-saline soils in their survival and symbiotic behaviour under saline conditions (Bharadwaj, 1975).

Susceptibility of the rhizobial symbiosis to salinity in legumes does not appear to be a generalized phenomenon. In Prosopis tamarago, a tree legume, symbiotic nitrogen fixation was not affected with increasing salinity, even at 3.6% NaCl (Felker et al., 1981). Nodulation of alfalfa was relatively resistant to salinity, whereas nodulation of soybean was extremely sensitive to salinity (Bernstein and Ogatta, 1966). Mungbean was more sensitive than cowpea with respect to salinity effects on nodulation and nitrogen fixation (Balasubramanian and Sinha, 1976). In Trifolium alexandrinum, salinity did not affect nodulation and nitrogen fixation (Bharadwaj, 1975), whereas it suppressed nodulation and nitrogen fixation in Vicia faba (Yousef and Sprent, 1983).

Susceptibility of the rhizobial symbiosis to salinity stress can also vary depending on the particular salt. In lucerne, 0.7% NaCl totally suppressed nodule formation, whereas successful nodulation and nitrogen fixation was possible at 1% KCl and MgCl2 (Singh et al., 1973). Even though lucerne could tolerate up to 3% NaCl, nodulation was affected from 0.4% NaCl onwards with total suppression of nodulation at 0.7%. This suggests that the limits of salinity for good nodulation and nitrogen fixation are different from the limits for the Rhizobium and the host individually, at least in some legumes.

2.6 Genetics of salinity tolerance

Salinity tolerance is probably the expression of a number of genes and the importance of the expression of each is dependent upon its interaction with other salt tolerance genes and the external salt concentrations (Shannon, 1985). Tolerance to salt, water deficit or other stresses are considered 'complex' characteristics (Ramage, 1980; Woolhouse, 1981). Information on the genetic control of physiological processes is required for understanding the stability or instability of the genotypic performances over a range of environmental conditions (Tal, 1985).

Based on a diallel cross of six varieties of Oryza sativa (two tolerant, two moderately tolerant and two susceptible to salinity) and their F1 hybrids (evaluated at 12 dS/m salinity level) it was found that genes controlling sodium and calcium levels in the shoot were partially dominant. At least three groups of genes were believed to be involved in the inheritance of sodium and calcium levels (Akbar et al., 1986). Glycinebetaine which accumulates in several plant families during salinity stress and mainly has a role in osmotic adjustment at the cellular level, was found to be controlled by a small group of genes likely to be an additive trait (Grumet et al., 1985). In studies with Festuca rubra, Venables and Wilkins (1978) reported that the salinity tolerance trait was a dominant genetic factor.

Elytrigia elongata, a wild wheat grass, was found to show high salinity tolerance compared to the cultivated wheat (T. aestivum). The salinity tolerance trait was expressed in the amphidiploid of T.

aestivum X E. elongata indicating that this is a dominant genetic factor (Dvorak and Ross, 1986). By transferring five chromosomes and a telosome from E. elongata to T. aestivum in the BC2F4 derivatives, it was found that the tolerance trait was expressed in these derivatives which could grow to maturity even at 35 dS/m salinity similar to the tolerant parent E. elongata (Dvorak et al., 1985). Storey et al. (1985) working on the same material concluded that in the wild type E. elongatum, efficient sodium regulation capacity in the shoot was responsible for its higher tolerance than the cultivated type T. aestivum. This was expressed in the amphiploids of T. aestivum X E. elongata indicating that this physiological trait is a dominant genetic factor. In studies with Aegilops squarrosa, Shah et al. (1987) reported that the "D" genome had a major role in improving K/Na selectivity under saline conditions and this was responsible for its higher tolerance to salinity than T. aestivum.

Akbar and Yabuno (1975) in their studies with rice varieties 'Jhona 349' (tolerant) and 'Magnolia' (susceptible), which differed in tolerance to salinity, found that the tolerance trait was expressed in the F1 hybrids. In soybean, chloride exclusion from the shoot was found to be controlled by a single gene pair and Abel (1969) proposed the gene symbols NCl and nCl as the dominant chloride excluder and the recessive as the chloride includer, respectively. In studies with wild relatives of Lycopersicon esculentum namely L. cheesmani, L. peruvianum and Solanum pennellii, it was found that these wild relatives had a higher level of tolerance to salinity than the cultivated tomato (L. esculentum) (Tal and Shannon, 1983). A positive correlation between sodium levels in the shoot and the level

of tolerance to salinity, which was believed to be a typical halophytic feature, was responsible for their higher level of tolerance, and sodium probably substitutes for potassium in at least some of its physiological functions (Tal and Shannon, 1983). These physiological characterstics were expressed in the F1 hybrids of L. esculentum X S. pennellii, whereas with L. cheesmani only the lower levels of potassium under salinity were found to be dominant over L. esculentum.

3. MATERIALS AND METHODS

3.1. Seed source: The source of different pigeonpea genotypes and wild relatives of pigeonpea which were used in the various experiments are listed in Table 3.1.

3.2. Seed treatment: Pigeonpea seeds were surface sterilised with 0.2% HgCl2 solution for five minutes, and then thoroughly washed with deionised water. Seeds of Atylosia, Dunbaria and Rynchosia species required special treatment to ensure germination and establishment. To promote germination, these seeds were scarified by nicking the testa with a scalpel, following which these seeds were surface sterilised and germinated on water absorbant blotting paper. The 'germination rolls' were prepared from these blotting papers (15 X 10 cms) in which the seeds were arranged on the central section and then rolled up. These "germination rolls" were placed in plastic bags, moistened with distilled water and then placed in an incubator at about 28 C. (Germination took usually between 5 and 7 days).

3.3 Plant culture

3.3.1. Hydroponic system: The surface sterilized pigeonpea seeds were sown in growth pouches (blotting paper envelope within a polythene bag) by placing 10 seeds in the cleft of each pouch and were held in position in perspex tanks (90 X 75 X 50 cms) by two brass rods passing through top corners of the pouches (Plate 1a and 1b). The bottom corners of growth pouch were cut to expose a portion of the blotting paper to nutrient solution in the tank. The outer surface of the

Table 3.1 Source of pigeonpea genotypes and wild relatives of pigeonpea used in the experiments.

Species	Genotype/ Accession No.	Source	Place of collection/ Remark
Cajanus cajan	ICP 8591 to 95	GRU, ICRISAT	from U.P, India
	ICP 8620 to 30	,,	,,
	ICP 8641 to 45	,,	,,
	ICP 8658 to 65	,,	,,
	ICP 8667 to 70	,,	,,
	ICP 10101 to 116	,,	,,
	ICP 11766	,,	,,
	ICP 11772	,,	,,
	ICP 11795 to 96	,,	,,
	ICP 11798 to 802	,,	,,
	ICP 11847 to 55	,,	,,
	ICP 11862 to 79	,,	,,
	ICP 9120	,,	,,
	ICP 9144	,,	,,
	ICP 9182	,,	,,
	ICP 9169	,,	,,
	ICP 9190	,,	,,
	ICP 9199	,,	,,
	ICP 6888	,,	,,
	ICP 4043	,,	,,
	ICP 4404	,,	,,
	ICP 11691	,,	,,
	ICP 11679	,,	,,
	ICP 11684	,,	,,
	ICP 11690	,,	,,
	ICP 10965	,,	Punjab
	ICP 9012	,,	Maharashtra
	ICP 12211	,,	,,
	ICP 13006	,,	Orissa
	ICP 13010	,,	,,
	ICP 8012	,,	,,
	ICP 8010	,,	,,
	ICP 8007	,,	,,
	ICP 8008	,,	,,
	ICP 8009	,,	,,
	ICPL 270	Breeding	Breeders line
	ICPL 366	Pigeonpea-	Breeders line
	ICPL 304	breeding unit	,,
	ICPL 248	ICRISAT	,,
	ICPL 228	,,	,,
	ICPL 247	,,	,,

contd.

Table 3.1 continued

Species	Accession No.	Source	Place of collection/ Remarks
	BAHAR	,,	,,
	ICPL 8309	,,	,,
	ICPL 8312	,,	,,
	ICPL 8317	,,	,,
	IPCL 8320	,,	,,
	ICPL 286	,,	,,
	ICPL 233	,,	,,
	ICPL 112	,,	,,
	ICPL 8304	,,	,,
	ICPL 8340	,,	,,
	ICPH 6	,,	,,
	ICPL 329	,,	,,
	ICPL 306	,,	,,
	ICPL 186	,,	,,
	ICPL 138	,,	,,
	BDN 1	,,	,,
	M 59	,,	,,
	BWR 370	,,	,,
	HY 4	,,	,,
	RRG 5	,,	,,
	ICPL 95	,,	,,
	ICPL 268	,,	,,
	ICPL 8322	,,	,,
	ICPL 8326	,,	,,
	ICPL 84018	,,	,,
	ICPL 227	Breeding	-
	HY 3C	,,	-
	ICP 3783	GRU, ICRISAT	-
Atylosia platycarpa	jm 2873	,,	-
A. scarabaeoides	jm 1965	,,	-
A. albicans	jm 2337	,,	-
A. acutifolia	ibs 2479a	,,	-
A. cajanifolia	pr 4876	,,	-
A. goensis	jm. 3501	,,	-
A. grandifolia	ec. 124363	,,	-
A. lineata	jm 3366	,,	-
A. lanceolata	ec. 137220	,,	-
A. mollis	jm. 4331	,,	-
A. reticulata	ebs. 2156	,,	-
A. sericea	jm. 1961	,,	-
A. vlubilis	jm. 1984	,,	-
Rynchosia albiflora	nkr 143	,,	,,
Dunbaria ferruginea	jm 2317	,,	,,
A. albicans X ICP 3783	F1 hybrid seed	,,	-

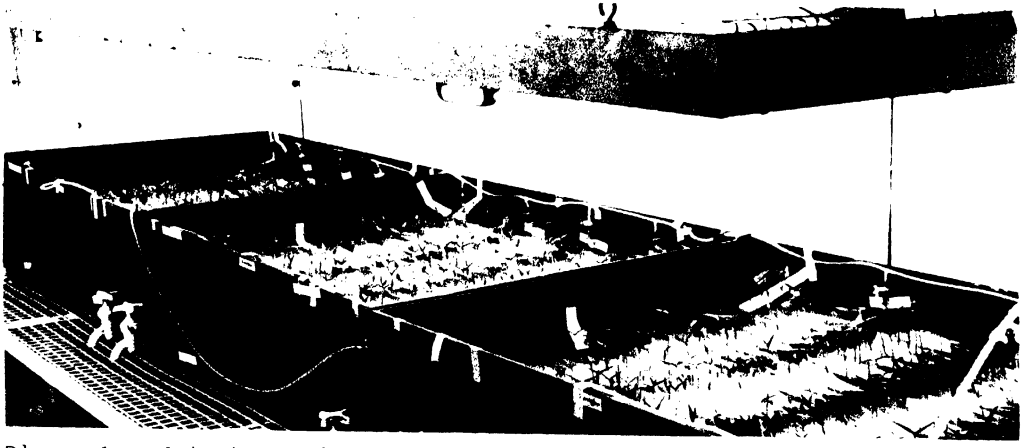

Plate 1a. A hydroponic screening system for evaluation of pigeonpea genotypes for salinity tolerance.

Plate 1b. Arrangement of growth pouches in the hydroponic system.

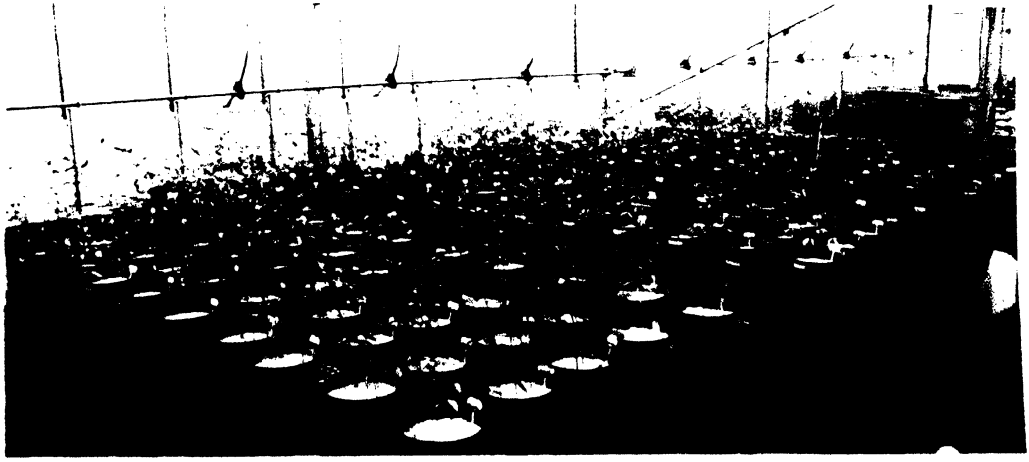

Plate 1c. A sand culture system to study the response of pigeonpea

perspex tanks were painted black to prevent algal growth in the solutions. For the control treatment, a modified Arnon and Hoagland solution (Table 3.2) with 50 ppm nitrogen as ammonium nitrate was used. For salinity treatments, the nutrient solution was amended with NaCl + CaCl2 (1:1 w/w) to give the required electrical conductivity (ECe). One hundred litres of respective treatment solutions were supplied to each tank from the time of sowing and the nutrient solution was aerated throughout the experimental period. Solutions were monitored at the end of each day for ECe and adjusted to the required treatment level by adding an appropriate amount of deionised water. Treatment solutions in the tanks were replaced every week. The tanks were covered with black cotton cloth for about 7 days after sowing to facilitate seed germination and seedling emergence and seedlings were thinned to five per pouch at the end of the 10th day. The experiments were arranged in a split-plot design with salt treatment as the main plot, and genotype as sub-plot. These experiments were conducted in the greenhouse (day temp, 28 + 2 C; night temp, 22 + 2C; and relative humidity, 60-70%) and also in a controlled environment growth chamber (day temp 28 + 2 C, night temp 22 + 2 C, relative humidity, 60-70%; light intensity, 500 lux;, photoperiod, 14 h).

3.3.2 Sand culture system: The growth medium consisted of sieved river sand, which was washed, soaked in acid solution (pH 1-2) for 24 hours, and thoroughly washed with tap water, dried and filled into 6 in. diameter pots (Fig 1c). The pots with sand were steam sterilized. In each pot, 8 seeds were sown. In case of wild species (Atylosia, Rynchosia and Dunbaria) the pregerminated seeds were planted in the

Table 3.2 Composition of Arnon and Hoagland nutrient solution

Compound	mg/L	For stock solution (g/L)	
1. KH_2PO_4	122	12.2	}
KCl	155	15.5	} 100 times
$MgSO_4 \cdot 7H_2O$	250	25.0	}
2. $CaCl_2 \cdot 2H_2O$ or	215	21.5	}
($CaSO_4 \cdot 2H_2O$)	(250)	(25.0)	} 100 times
3. $MnSO_4 \cdot H_2O$	1	1.0	}
$ZnSO_4 \cdot 7H_2O$	0.25	0.25	}
$CuSO_4 \cdot 5H_2O$	0.25	0.25	}
H_3BO_3	0.25	0.25	}
$Na_2MoO_4 \cdot 2H_2O$	0.05	0.05	} 1000 times
4. $FeC_6H_5O_7 \cdot 5H_2O$	30	30	} 1000 times
(Ferric citrate) or			
($FeCl_3$) or	(15)	(15)	
Na Fe EDTA	(59)	(59)	

To make 1L of nutrient solution, take the stock solution No.1, 10 ml; No.2, 10 ml; No. 3, 1 ml; No. 4, 1 ml and add to 1000ml of deionised water. Adjust the pH of the nutrient solution to 6.5 with either 1 N NaOH or 1N HCl.

Table 3.3 Origin and growth characterstics of pigeonpea *Rhizobium* cultures used for salt tolerance study.

Sl. No.	*Rhizobium*	Soil type	Growth on YEM agar plates
1.	IC 3024	Black soil	F a
2.	IC 3506	Saline	F
3.	IC 3484	Black soil	S b
4.	IC 3087	Saline	S
5.	IC 3195	Red soil	S

a. Fast grower b. Slow grower

pots. The sand surface in each pot was covered with 50 g sterilized polythene beads in order to minimize evaporational water loss. Pots were supplied with deionised water until 13 days. On the tenth day after sowing, seedlings were thinned to 4 per pot. These experiments were arranged in a randomized block design with four replications. A modified Arnon and Hoagland nutrient solution (1/4th strength) with 50 ppm nitrogen as ammonium nitrate was used for watering the plants for the control treatment (see Table 3.2). This solution was amended with sodium chloride and calcium chloride (1:1 w/w) for salinity treatments. The experiments were conducted in a greenhouse (day temperature, 28 + 2 C, night temperature, 22 + 2 C and relative humidity, 60-70%). On the fourteenth day after sowing, the pots were flushed with one litre of treatment solution. The salt treatments above 4 dS /m salinity level were increased at 2 ds /m per day so as to avoid any shock to the plants; the final concentration of 10 or 12 ds/m was reached 4 or 5 days after imposing salinity treatments. Pots were flushed with respective treatment solutions at 250 ml/pot on every alternate day to avoid salt accumulation in the pots. Compensation for evapotranspirational water losses was made every day by adding an appropriate amount of deionised water after weighing the pots. The pH of the treatment solutions was adjusted to 6.5. Pots were randomized once in every three days to minimize spatial microenvironmental effects in the glasshouse. Fallen leaves were collected from time to time and were included in dry weight estimations and for chemical analysis.

3.4. Observations and measurements: Germination was recorded at the end of the seventh day after sowing. Leaf area was measured with an

automatic leaf area meter (Delta- T devices limited, England). For shoot dry weight, plant tops were dried at 70 C for 48 h and weighed using a Mettler AE 166 balance. For root dry weight, roots were carefully removed from pots and then cleaned of sand by deionised water. These were dried at 70 C for 48 h and then dry weights were recorded. The transpiration rate was recorded from the first fully expanded trifoliate leaf between 11-12 am using a Steady State Porometer (LICOR, Inc. LI- 1600).

3.5 Biochemical analysis

3.5.1. Proline estimation: The first fully expanded trifoliate leaf was collected in a 'zip-lock' polythene bag and immediately stored at -11 C for proline determination (Bates, 1973). Approximately 500 mg of leaf material was homogenized in 10 ml of 3% aqueous sulfosalicylic acid and the homogenate filtered through Whatman No 2 filter paper. Two ml of filtrate was reacted with 2 ml of acid ninhydrin and 2 ml of glacial acetic acid in a test tube at 100°C in a water bath for one hour and the reaction was terminated in an ice bath. The reaction mixture was extracted with 4 ml of toluene and mixed vigorously with a test tube stirrer for 15 to 20 seconds. The chromophore containing toluene was aspirated from the aqueous phase, warmed to room temperature and the absorbance read at 520 nm using toluene as a blank. The proline concentration was determined from a standard curve and calculated on a fresh weight basis using the following formula:
mmoles proline/g fresh weight. = [(mg proline/ml X ml toluene)/115.5 mg/mmole]/ [(g sample)/5].

3.5.2. Nitrogen and Phosphorus estimation: For various estimations leaf, stem and root samples were finely ground by a Cyclone mill (UDY Corporation, Colorado, USA). Finely ground plant samples of 100 to 150 mg were digested by adding 4 ml of concentrated sulphuric acid containing 0.5% (w/v) selenium and heating on a hot plate at 360 C for 1.5 hrs. After digestion, the sample was diluted by making it up to 75 ml with glass-distilled water. Three ml of this diluted digest was fed to an autoanalyser (Technicon autoanalyzer II, Technicon industrial systems, Tarrytown, New York) and analyzed for nitrogen and phosphorus contents following Technican Autoanalyser industrial method No.144-71a.

3.5.3. Determination of Na, K, Ca, Mg, Zn, Mn and Fe: Finely ground plant samples of 200 to 300 mg were digested with 6 ml of tri-acid (HNO_3 : H_2SO_4 : $HClO_4$ at 10:0.5:2) in a sand bath at 250 C for 6 to 8 h (Piper, 1952) in 50 ml volumetric flasks. The digested plant samples were diluted to 50 ml by glass distilled water and this sample was analysed in an atomic absorption spectrophotometer (model 1200) for the determination of Zn, Mn, and Fe. One ml of the diluted digest was transferred to a 25 ml volumetric flask, 0.5 ml lanthanum chloride (50,000 ppm) was added and the solution made up to volume with glass distilled water. This sample was fed to the atomic absorption spectrophotometer for the estimation of Na, K, Ca and Mg.

3.5.4. Chloride estimation: The chloride content was determined by the Mohr volumetric method (Piper, 1952). As the equivalence point was passed, the excess of silver combines with the chromate to form a reddish brown precipitate of silver chromate. About 500 mg of finely

ground plant sample was shaken in 50 ml of 2% calcium nitrate for 15 minutes and the mixture was treated with 250 mg of activated charcoal (chloride free) before filtration through Whatman No 2 filter paper. Five ml of the filtrate was titrated with 0.025 N AgNO3 using potassium chromate as indicator. The chloride content in the plant sample was calculated according to the following formula:

Cl (%) = ml of AgNO3 X 10 X 886.25 /Wt of the sample (gms) X 10,000

3.6 Rhizobium inoculation, nodulation and nitrogen fixation

3.6.1 Rhizobium culture production: The rhizobial cultures IC 3024, IC 3506, IC 3484, IC 3087 and IC 3195 were obtained from the pigeonpea Rhizobium culture collection of Pulse Agronomy, ICRISAT center, Patancheru, India. They were all effective in fixing nitrogen in symbiosis with pigeonpea. The origin and growth habit of the Rhizobium cultures used are presented in Table 3.3. All cultures were maintained on yeast extract mannitol agar slopes (Vincent, 1977). Yeast-extract mannitol broth medium (YEM) was prepared and distributed into 250 ml conical flasks @100 ml/flask. The composition of YEM (g/L) was : mannitol 10.0, K2HPO4 0.5, MgSO4 7H2O 0.2, NaCl 0.1, yeast extract 0.5, distilled water 1000ml. The pH was 6.8. The YEM in conical flasks was autoclaved at 15 lbs/sq. inch pressure for 20 minutes and cooled to room temperature. A loopful of rhizobial culture was inoculated into the sterilized YEM broth and incubated at 28 C for 3 and 7 days for fast- and slow-growing strains, respectively. After incubation the culture was checked for purity by streaking a loopful of the broth culture on Congo red yeast-extract mannitol agar and incubating at 28 C.

3.6.2. Rhizobial inoculation: For all rhizobial inoculation treatments, one ml of rhizobial broth containing atleast 10-7 cells/ml was used per seedling or seed at sowing . Rhizobial inoculation was repeated after 3 days to ensure sufficient rhizobial population in the pot.

3.6.3. Acetylene reduction assay: The nodulated roots were carefully removed from the pots and assayed for nitrogenase activity by the acetylene reduction technique (Dart et al., 1972). The excised roots and nodules were placed in 300 ml air tight glass container. After a 30 min incubation in 10% atmosphere of C2H2 at ambient air temperature in the glasshouse, a 3.5 ml gas sample was removed and stored in pre-evacuated 7 ml 'venoject' tubes (Terumo corporation, Tokyo, Japan). The sample was analyzed for ethylene and acetylene on a Pye-Unicam 104 gas chromatograph fitted with a flame ionization detector and a glass column 150 cm long and 0.6cm OD, packed with Poropak N. The oven temperature of the gas chromatograph was 100 C and the carrier gas (nitrogen) flow rate 45ml/min.

3.6.4. Nodule study: After the acetylene reduction assay, roots and nodules were thoroughly cleaned with deionised water. The nodules were separated and counted. Nodules were dried at 70 C for 48 h and dry weights recorded.

3.6.5. Statistical analysis: The data was analysed for 'anova' on the Vax 11/780 computer using genstat program.

4. RESULTS

4.1 Screening and selection of pigeonpea germplasm for salinity tolerance

The objective of this investigation was to assess the exploitable genetic variability in pigeonpea for salinity tolerance and to detect the salt tolerant pigeonpea lines from the germplasm. One hundred and fifty two pigeonpea lines, which include germplasm lines (collected from various salt affected districts of Uttar Pradesh, Orissa, Punjab and Maharashtra) and a number of breeders lines, were used in this study.

A hydroponic system was used to grow the plants and the experiment was replicated three times. There were two treatments: 1. control (non-stress) 2. 6 dS/m. Previous experience with pigeonpea indicated that 6 dS/m salinity stress is sufficient to separate the genotypic differences in pigeonpea. Plants were harvested on the 60th day from sowing and the accessions were rated based on their leaf necrosis status as follows: 1. without leaf necrosis, 2. with leaf necrosis.

Findings

Germination was significantly affected at 6 dS/m and was reduced from 86% (control) to 76%. However, there were significant differences among genotypes in this respect. In few pigeonpea lines (ICP 8695, ICP 11878, ICPL 228, ICPL 329, ICP 8007), the germination was as good as in the control. In all the pigeonpea lines tested,

germination at 6 dS/m salinity level was above 70% of their respective control indicating that the germination process in pigeonpea was fairly tolerant to this level of salinity; this conforms with our earlier studies with pigeonpea.

Salt burning symptoms, i.e leaf necrosis appeared, around 20 days after sowing and became severe in a number of genotypes by 60 days. There was considerable variation among genotypes in their survival at this salinity level. The survival was as good as in the control (i.e 100%) in a number of accessions, whereas there was over 70% mortality in a large number of accessions. ICP 8663 was one of the worst affected accessions with a 90% mortality. Based on growth performance (i.e shoot dry matter production at 6 dS/m salinity level, and survival (%)) the pigeonpea accessions were grouped into 3 categories (Table 4.1.1):

1. The first category includes accessions where shoot dry matter production was at least 50% or more of the respective control, with or without leaf necrosis, and survival (%) was more than 70%. There were 39 accessions in this category. Among these accessions, ICP 8594, ICP 8623, ICP 8658, ICP 8659, ICP 10103, ICP 11847, ICP 11863, ICP 11876, ICP 11690, ICPL 8317, ICPL 112 and ICPL 227 showed no leaf necrosis symptoms. Pigeonpea genotype ICPL 227, a breeders line was found to be the most promising as it produced a shoot dry matter of 71% of its control at 6 dS/m without leaf necrosis.

2. The second category includes accessions, where shoot dry matter production was between 30% and 50% of the respective control with or without leaf necrosis on majority of the plants. There were

Table 4.1.1. Effect of salinity (ECe 6 dS/m) on germination, survival and growth of pigeonpea genotypes

Sl.No.	Genotype	Germination (%)		Survival (%)	Shoot dry weight (mg/plant)		
		6 dS/m	% of control	6 dS/m	Control	6 dS/m	% of control
				Category I			
1.	ICP 8592	73	88	86	317	170	54
2.	ICP 8594 *	75	90	100	659	377	58
3.	ICP 8595	80	93	100	367	194	53
4.	ICP 8622	80	89	73	363	185	51
5.	ICP 8623 *	73	88	80	320	171	53
6.	ICP 8626	67	84	100	380	260	58
7.	ICP 8658 *	73	88	93	366	202	55
8.	ICP 8659 *	77	93	100	454	240	58
9.	ICP 8661	73	91	100	200	109	55
10.	ICP 8695	80	100	100	258	132	51
11.	ICP 8704	63	79	100	247	136	55
12.	ICP 9076	73	88	73	187	107	57
13.	ICP 9077	73	78	86	180	90	50
14.	ICP 9092	83	92	100	320	170	53
15.	ICP 10103 *	73	78	86	390	240	61
16.	ICP 10110	73	84	80	403	201	50
17.	ICP 10112	77	86	100	289	170	59
18.	ICP 11798	73	84	97	220	117	53
19.	ICP 11802	77	83	80	173	93	54
20.	ICP 11847 *	77	83	91	288	147	51
21.	ICP 11863 *	77	83	73	162	90	56
22.	ICP 11867	77	83	86	229	115	51
23.	ICP 11874	70	80	93	260	137	53
24.	ICP 11876 *	73	78	100	287	165	57
25.	ICP 11877	70	78	93	393	207	52
26.	ICP 11878	77	100	76	327	170	52
27.	ICP 9199	75	89	73	203	103	51
28.	ICP 4404	70	80	80	233	122	52
29.	ICP 11684	77	83	93	373	200	54
30.	ICP 11690 *	77	83	93	403	210	52
31.	ICPL 270	85	94	80	379	181	58
32.	ICPL 366	77	86	93	383	213	56
33.	ICPL 8309	77	89	80	297	148	50
34.	ICPL 8317 *	80	89	93	287	160	56
35.	ICPL 112 *	80	92	80	567	287	51
36.	ICPH 6	77	96	93	296	159	54
37.	ICPL 186	80	100	86	270	143	53
38.	BDN 1	83	95	86	345	177	51
39.	ICPL 227 *	85	94	93	352	256	71

contd.

Table 4.1.1 contd.

Sl.No.	Genotype	Germination (%)		Survival (%)	Shoot dry weight (mg/plant)		
		6 dS/m	% of control	6 dS/m	Control	6 dS/m	% of control
				Category 2			
40.	ICP 8591	73	91	86	304	148	41
41.	ICP 8593	83	92	80	362	178	49
43.	ICP 8620	73	84	72	207	92	44
44.	ICP 8621	87	97	52	377	161	43
45.	ICP 8625	86	92	80	160	68	43
46.	ICP 8627	87	97	40	253	78	31
47.	ICP 8630	73	91	46	329	114	35
48.	ICP 8641	77	89	100	333	162	45
49.	ICP 8644	80	89	100	209	89	42
50.	ICP 8645	77	89	100	188	62	33
51.	ICP 8660	77	86	72	240	77	33
52.	ICP 8662	73	95	100	183	81	48
53.	ICP 8665	67	81	10	187	65	35
54.	ICP 8668	80	96	53	214	82	38
55.	ICP 8670	70	88	73	210	69	32
56.	ICP 8672 *	73	88	100	283	103	37
57.	ICP 8673	80	91	46	263	97	37
58.	ICP 8697	70	88	66	277	93	34
59.	ICP 8699	77	86	93	233	111	48
60.	ICP 8700	75	90	66	234	78	33
61.	ICP 8702	67	87	46	206	60	30
62.	ICP 8709 *	63	78	100	303	147	47
63.	ICP 9059	63	72	100	283	124	45
64.	ICP 9078 *	73	88	86	253	117	47
65.	ICP 9079	77	89	33	203	75	37
66.	ICP 9093 *	77	93	100	381	161	43
67.	ICP 9094	77	89	73	257	112	48
68.	ICP 9095	70	80	53	235	86	37
69.	ICP 10099	83	86	100	287	130	45
70.	ICP 10102	77	89	33	134	44	34
71.	ICP 10108	70	80	66	243	108	45
72.	ICP 10109	77	89	73	583	180	31
73.	ICP 10111	73	81	93	270	119	45
74.	ICP 10115	77	89	33	317	93	43
75.	ICP 11800	83	89	46	177	78	45
76.	ICP 11801	77	89	68	415	137	33
77.	ICP 11848	70	91	73	251	117	46
78.	ICP 11849	70	78	33	193	69	37
79.	ICP 11852	70	78	33	218	66	32

contd.

Table 4.1.1 contd.

Sl.No.	Genotype	Germination (%)		Survival (%)	Shoot dry weight (mg/plant)		
		6 dS/m	% of control	6 dS/m	Control	6 dS/m	% of control
80.	ICP 11853	77	86	46	351	109	31
81.	ICP 11865	67	81	33	165	60	35
82.	ICP 11866	80	92	66	226	91	41
83.	ICP 11868	77	83	26	243	82	35
84.	ICP 11869	80	86	73	161	73	45
85.	ICP 11871	70	84	20	373	137	37
86.	ICP 11873	70	80	53	240	93	39
87.	ICP 11879	80	89	73	423	131	31
88.	ICP 9144	77	79	46	339	120	35
89.	ICP 9182	77	89	46	386	128	35
90.	ICP 6888	77	89	33	193	86	44
91.	ICP 4043	77	83	66	332	117	35
92.	ICP 11691 *	77	93	80	398	161	41
93.	ICP 11679	77	89	80	448	171	38
94.	ICP 304	80	96	46	313	94	30
95.	ICPL 248	77	96	40	386	127	33
96.	ICPL 228 *	77	100	86	303	121	40
97.	ICPL 247	85	92	73	413	148	36
98.	ICPL 8312	70	78	46	245	76	31
99.	ICPL 8320	77	89	46	385	184	48
100.	ICPL 286	77	96	40	355	114	33
101.	ICPL 233	73	88	66	440	198	45
102.	ICPL329	83	100	80	290	121	42
103.	ICPL 138	80	96	46	197	70	37
104.	BWR 370 *	83	92	93	280	137	49
105.	ICPL 95	80	95	40	427	135	32
106.	ICPL 268	75	86	40	203	63	32
107.	ICPL 8326	73	95	80	407	154	38
108.	ICPL 84018	77	95	46	236	100	43
109.	ICP 10965	77	83	66	187	77	41
110.	ICP 12211	77	93	46	288	92	32
111.	ICP 13006	70	80	66	222	93	42
112.	ICP 13010	80	86	26	243	96	39
113.	ICP 8008	67	87	53	471	142	30
114.	ICP 8624	70	80	100	338	164	49
				Category III			
115.	ICP 8629	73	78	20	367	87	24
116.	ICP 8642	70	84	25	421	88	21
117.	ICP 8663	67	92	10	373	58	16
118.	ICP 8671	76	99	33	267	52	20
119.	ICP 8696	73	84	46	361	71	20

contd.

Table 4.1.1 contd.

Sl.No.	Genotype	Germination (%)		Survival (%)	Shoot dry weight (mg/plant)		
		6 dS/m	% of control	6 dS/m	Control	6 dS/m	% of control
120.	ICP 8698	73	95	40	248	47	19
121.	ICP 8703	67	84	30	242	55	23
122.	ICP 8705	63	72	46	267	60	23
123.	ICP 9058	63	76	30	261	70	27
124.	ICP 9072	63	76	35	314	90	29
125.	ICP 9074	67	81	33	254	69	27
126.	ICP 9080	77	89	26	217	63	29
127.	ICP 9081	73	88	26	210	66	26
128.	ICP 10098	80	89	26	291	70	24
129.	ICP 10106	77	96	40	273	60	22
130.	ICP 10116	77	83	30	294	76	26
131.	ICP 11766	80	89	33	433	122	28
132.	ICP 11772	80	82	35	288	60	21
133.	ICP 11795	75	83	40	254	36	15
134.	ICP 11796	70	80	26	303	46	15
135.	ICP 11799	80	86	26	237	48	20
136.	ICP 11850	70	75	35	335	97	29
137.	ICP 11870	70	82	26	240	68	28
138.	ICP 11875	80	84	46	320	75	23
139.	ICP 9120	80	86	26	465	99	21
140.	ICP 9169	87	97	46	430	87	22
141.	ICPL 8304	77	83	26	383	76	19
142.	ICPL 8340	70	80	20	310	73	25
143.	ICPL 306	77	89	26	403	91	23
144.	M 59	73	88	40	277	77	27
145.	HY 4	77	93	35	547	109	20
146.	RRG 5	75	88	26	213	39	18
147.	ICPL 8322	83	95	46	377	68	18
148.	ICP 9012	77	83	46	230	63	27
149.	ICP 8012	75	83	20	255	62	25
150.	ICP 8010	80	94	40	363	70	20
151.	ICP 8007	80	100	46	185	42	22
152.	HY 3C	72	88	25	351	55	16
153.	ICP 3783	80	89	30	450	90	20

For germination : SE + 3.84 : LSD % at 5% = 10.6 : CV % = 8.2
For survival : SE + 2.0 : LSD % at 5% = 5.5 : CV % = 8.5
For shoot dry matter : SE + 13.5 : LSD at 5% = 37.4 : CV% = 11.2
For shoot dry matter (% of control): SE + 2.85 : LSD at 5% = 7.9 : CV% = 7.1
* No leaf necrosis (accessions without asterik showed leaf necrosis)

68 accessions in this category. The survival in this group varied from 100% in 9 accessions (ICP 8641, ICP 8644, ICP 8645, ICP 8662, ICP 8672, ICP 8709, ICP 9059, ICP 9093, ICP 10099) to 10% in ICP 8665. In 7 accessions, (ICP 8672, ICP 9078, ICP 9093, ICP 11691, ICPL 228 and BWR 370) there was no leaf damage symptoms on any of the plants. In the remaining accessions of this group, leaf necrosis symptoms appeared on the majority of the plants.

3. The third category comprises pigeonpea lines where shoot dry matter production was less than 30% of the respective control with leaf necrosis symptoms on a majority of the plants. The survival in this group was less than 50% of the control.

4.2. Effect of different levels of salinity on selected genotypes

The response of some of the pigeonpea genotypes selected for tolerance ,(ICP 8594, ICP 8659, ICP 10103, ICPL 112 and ICPL 227) or sensitivity (ICP 8663, ICP 3783, ICP 9080, ICP 11772, and HY 3C) to salinity in Expt 4.1 was examined over a range of salinity levels. It was intended to determine if there was any relation between the proline accumulation of leaves and salinity tolerance. A hydroponic system was used to grow the plants and the experimental conditions and design were essentially the same as Expt. 4.1 except this was replicated 4 times and conducted in a controlled environmental growth chamber. There were six salinity treatments: 0, 5, 6, 7, 8 and 9 dS/m.

None of the pigeonpea lines survived beyond 30 days at 8 and 9 dS/m salinity levels. Leaf samples were collected 40 days after sowing for free proline determination. The plants were harvested 50 days after sowing and rated for necrosis damage as described in Expt. 4.1.

Findings:

Germination was significantly affected with increasing salinity in the medium (Table 4.2.1). Germination was reduced from 90% (control) to 80%, 74%, 69%, and 60% at 5, 6, 7, 8, 9 dS/m salinity levels respectively. Alhough the germination of a few tolerant lines like ICP 8594 and ICPL 227 was superior to that of some susceptible lines like HY 3C, the other susceptible lines were no different from the tolerant lines in germination at any of the salinity levels.

Table 4.2.1. Effect of different levels of salinity on germination (%) of selected pigeonpea genotypes.

Sl.No.	Genotype	Salinity treatment (ECe dS/m)					
		0	5	6	7	8	9
1.	ICP 8594	85	85 (100)	75 (88)	75 (88)	70 (82)	70 (82)
2.	ICP 8659	90	78 (87)	75 (83)	70 (78)	65 (72)	60 (67)
3.	ICP 10103	95	85 (89)	73 (77)	75 (79)	70 (74)	65 (68)
4.	ICPL 112	95	83 (87)	75 (79)	70 (74)	65 (68)	60 (63)
5.	ICPL 227	90	85 (94)	85 (94)	75 (83)	70 (78)	70 (78)
6.	ICP 8663	80	75 (94)	70 (88)	63 (79)	60 (75)	55 (69)
7.	ICP 3783	85	70 (82)	63 (74)	58 (68)	50 (59)	40 (47)
8.	ICP 9080	90	78 (87)	75 (83)	70 (78)	65 (72)	60 (67)
9.	ICP 11772	90	80 (89)	70 (78)	65 (72)	60 (67)	60 (67)
10.	HY 3C	95	80 (84)	80 (84)	70 (74)	65 (68)	60 (63)

SE ± 3.73 : LSD at 5% = 10.44 : CV% = 9.6
Note: Figures in parenthesis are '% of control'

Table 4.2.2. Effect of different levels of salinity on the survival (%) and leaf damage (LD) of selected pigeonpea genotypes.

Sl.No	Genotype	Salinity treatment (ECe dS /m)							
		0		5		6		7	
		Survival	LD	Survival	LD	Survival	LD	Survival	LD
1.	ICP 8594	100	A	100	A	100	A	90	A
2.	ICP 8659	100	A	100	A	93	A	93	A
3.	ICP 10103	100	A	100	A	95	A	90	A
4.	ICPL 112	100	A	100	A	80	A	70	A
5.	ICPL 227	100	A	100	A	100	A	93	A
6.	ICP 8663	100	A	100	A	30	B	10	B
7.	ICP 3783	100	A	100	A	40	B	20	B
8.	ICP 9080	100	A	100	A	15	B	10	B
9.	ICP 11772	100	A	100	A	35	B	20	B
10.	HY 3C	100	A	100	A	30	B	20	B

SE ± 2.65 : LSD at 5% = 7.43 : CV% = 6.8
LD - Leaf damage, A - without leaf necrosis, B - with leaf necrosis

At 8 and 9 dS/m salinity levels, leaf necrosis symptoms appeared by 15 days and none of the pigeonpea lines were able to survive beyond 30 days. At 6 and 7 dS/m salinity levels, leaf necrosis symptoms appeared by 20 days in the least tolerant lines and became severe by 50 days (Table 4.2.2).

At 5 dS/m salinity level, leaf necrosis symptoms were not apparent and there was no mortality in any of the pigeonpea lines tested. At 6 and 7 dS/m salinity levels, leaf necrosis symptoms appeared in all the five least tolerant lines and there was more than 50% mortality in a majority of the lines. In contrast, none of the most tolerant lines showed any leaf necrosis symptoms and the survival was more than 90% except in ICPL 112, where there was 30% mortality at 7 dS/m.

Leaf area and shoot dry matter production were significantly decreased with increasing salinity (Table 4.2.3). However, the relative reduction of leaf area and shoot dry matter at various salinity levels was less in the most tolerant lines compared to the least tolerant lines. At 5 dS/m salinity level, the differences between the most and least tolerant lines were not clear but at 6 and 7 dS/m salinity levels the differences in leaf area and shoot dry matter between the most and least tolerant lines were significant. Among the most tolerant lines, ICPL 227 was superior in leaf area and shoot dry matter production (% of control) at various salinity levels. Among the least tolerant lines, HY 3C was most affected at various salinity levels.

Table 4.2.3. Effect of different levels of salinity on leaf area, shoot dry matter and leaf proline content of selcted pigeonpea pigeonpea genotypes.

Sl.No	Genotype	Salinity treatment (ECe dS/m) 0	5	6	7
		Leaf area (cm2/plant)			
1.	ICP 8594	145	83 (57)	74 (51)	70 (48)
2.	ICP 8659	119	74 (62)	63 (53)	40 (50)
3.	ICP 10103	141	84 (60)	73 (52)	58 (41)
4.	ICPL 112	140	84 (60)	67 (48)	56 (40)
5.	ICPL 227	121	82 (68)	78 (64)	58 (48)
6.	ICP 8663	104	57 (55)	23 (22)	10 (10)
7.	ICP 3783	180	101 (56)	59 (32)	11 (6)
8.	ICP 9080	144	72 (50)	29 (20)	7 (5)
9.	ICP 11772	131	70 (53)	20 (15)	7 (5)
10.	HY 3C	140	56 (40)	21 (15)	7 (5)

SE ± 4.14 : LSD at 5% = 11.6 : CV% = 11.1
SE ± 2.24 (for % of control) : LSD at 5% = 6.28 : CV% = 8.2

		Shoot dry matter (mg/pot)			
1.	ICP 8594	725	439 (59)	388 (53)	363 (50)
2.	ICP 8659	955	575 (60)	525 (55)	459 (48)
3.	ICP 10103	662	429 (63)	330 (50)	264 (40)
4.	ICPL 112	741	446 (60)	355 (48)	312 (42)
5.	ICPL 227	558	391 (70)	362 (65)	277 (50)
6.	ICP 8663	544	326 (60)	162 (30)	96 (18)
7.	ICP 3783	725	370 (51)	255 (35)	107 (15)
8.	ICP 9080	600	300 (50)	180 (30)	31 (5)
9.	ICP 11772	690	352 (51)	140 (20)	70 (10)
10.	HY 3C	646	265 (41)	122 (19)	65 (10)

Note: Figures in parenthesis are '% of control'
SE ± 33.3 : LSD at 5% = 93.1 : CV% = 17.0
SE ± 2.74 (for % of control) : LSD at 5% = 7.68 : CV% = 9.7

		Leaf proline content (mg/g fresh wt)			
1.	ICP 8594	1.43	1.73	1.80	3.80
2.	ICP 8659	1.47	1.84	2.07	3.07
3.	ICP 10103	1.62	1.98	4.33	6.55
4.	ICPL 112	1.28	1.89	2.78	5.48
5.	ICPL 227	1.67	1.77	1.88	2.89
6.	ICP 8663	2.21	2.43	3.08	5.15
7.	ICP 3783	1.70	1.91	2.28	3.46
8.	ICP 9080	1.35	1.68	2.73	3.95
9.	ICP 11772	1.37	1.77	2.68	4.53
10.	HY 3C	1.55	1.65	2.18	2.75

SE ± 0.154 : LSD at 5% = 0.43 : CV% = 12.1

Leaf free proline levels increased with increasing salinity (Table 4.2.3) in all of the pigeonpea lines irrespective of their tolerance status. In two of the lines, 8663 (least tolerant) and ICP 10103 (most tolerant), this increase was marginally superior compared to the other lines at various salinity levels. In the other least tolerant lines, the proline levels were comparable to the most tolerant lines at various salinity levels, indicating no clear relationship between proline accumulation in leaves and tolerance to salinity in pigeonpea.

4.3. Salinity tolerance of pigeonpea in relation to calcium: Response to substitution of calcium for sodium in pigeonpea genotypes differing in salinity tolerance - ionic relations and their relevance to salinity tolerance.

In view of the widely accepted role of calcium in membrane stabilization and specific ion uptake, this investigation was taken up in order to ascertain the role of calcium in the salinity tolerance of pigeonpea and its influence on the ionic relations. Since field salinity is a complex problem, and the sodium and calcium relative concentrations vary from place to place, genotypes selected for saline conditions should be able to perform uniformly across the various sodium and calcium concentrations likely to occur under field conditions. Two pigeonpea genotypes ICPL 227 (most tolerant) and HY 3C (least tolerant) were selected for this study to determine their relative growth responses and ion uptake behaviour across a range of sodium and calcium concentrations at two levels of salinity.

Two salinity levels, 6 and 8 dS/m were used in this study. Calcium was substituted for sodium up to a maximum of 50% so as to keep the ECe and osmotic concentrations within a salinity level constant. The chloride concentration was therefore also maintained constant within a particular salinity level, irrespective of the sodium/calcium status of the treatment.

The concentrations of NaCl and CaCl2 for each of the calcium treatments are given in Table 4.3.1. A sand culture system was used for growing plants. The experiment was laid out in randomized complete block design with four replications. There were 12

treatments involving Ca : Na ratios at the salinity levels of 6 and 8 dS/m, as described in Table 4.3.1. The treatments were imposed on 14-day old seedlings and the plants were harvested 50 days after sowing.

Table 4.3.1 NaCl and CaCl2 required for various treatment solutions.

Salinity level	Calcium content	Salt composition	Ca/Na (mM)
I. Control	0.36 mM		
II. 6 dS/m			
	a. 0.36 mM Ca	59.3 mM NaCl + 0.36 mM CaCl2	165
	b. 1 mM Ca	58 mM NaCl + 1 mM CaCl2	58
	c. 5 mM Ca	50 mM NaCl + 5 mM CaCl2	10
	d. 10 mM Ca	40 mM NaCl + 10 mM CaCl2	4
	e. 15 mM Ca	30 mM NaCl + 15 mM CaCl2	2
III. 8 dS/m			
	a. 0.36 mM Ca	79.3 mM NaCl + 0.36 mM CaCl2	220
	b. 1 mM Ca	78 mM NaCl + 1 mM CaCl2	78
	c. 5 mM Ca	70 mM NaCl + 5 mM CaCl2	14
	d. 10 mM Ca	60 mM NaCl + 10 mM CaCl2	6
	e. 15 mM Ca	50 mM NaCl + 15 mM CaCl2	3
	f. 20 mM Ca	40 mM NaCl + 20 mM CaCl2	2

Note: In nutrient solution (Arnon's Hoagland 1/4th strength) the level of calcium is 0.36mM

FINDINGS:

At 6 dS/m, substitution of calcium for sodium from 0.36mM to 15mM increased the growth in both the genotypes ICPL 227 and HY 3C. Salt toxicity symptoms appeared at 0.36mM in the primary leaves of ICPL 227. In HY 3C, such symptoms were severe and spread to the trifoliate leaves in some plants. Growth was slightly improved at 1mM calcium level in both the genotypes, and salt toxicity symptoms disappeared in both the genotypes at the 5mM calcium level. Growth was generally

better as the calcium level in the medium increased.

At 8 dS/m with 0.36mM calcium, ICPL 227 was able to survive but there were leaf burning symptoms. HY 3C did not survive in this treatment. At 1mM calcium level, growth was improved in ICPL 227, but plants had mild salt damage symptoms. HY 3C did not improve at this calcium level. At 5mM calcium level, salt burning symptoms disappeared in ICPL 227 and growth was slightly improved with further increases in calcium concentration. HY 3C was able to survive at 5mM calcium level, but with salt damage symptoms. Growth was not visibly improved with further increases in calcium in the medium in both the genotypes.

4.3.1 Growth parameters: At 6 dS/m, substitution of calcium for sodium from 0.36mM to 15mM increased the leaf area from 29% of the control to 62% in ICPL 227 and from 20% of the control to 36% in HY 3C (Table 4.3.2). ICPL 227 was significantly superior to HY 3C at various calcium levels in the medium. At 8 dS/m, substitution of calcium for sodium from 0.36mM to 20mM increased the leaf area from 26% of the control to 40% in ICPL 227 and from 7% of the control to 13% in HY 3C. ICPL 227 was significantly superior to HY 3C at various calcium levels. Shoot and root dry matter also significantly increased with increasing calcium in the medium at 6 and 8 dS/m salinity levels in ICPL 227 and HY 3C (Table 4.3.2). The trends were similar to those of leaf area.

4.3.2 Ionic relations

Table 4.3.2. Effect of salinity with varying proportion of calcium and sodium on leaf area, shoot and root dry matter of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf area (cm2/pot)					
ICPL 227	994	6 dS/m	284 (29)	458 (46)	485 (49)	537 (54)	619 (62)	N.T
HY 3C	981	6 dS/m	201 (20)	267 (27)	294 (30)	341 (35)	349 (36)	
ICPL 227		8 dS/m	263 (26)	292 (29)	335 (34)	384 (39)	393 (40)	398 (40)
HY 3C		8 dS/m	64 (7)	79 (8)	87 (8.8)	119 (12)	123 (13)	128 (13)
SE ± 13.5			LSD at 5% = 38.04			CV% = 7.6		
			Shoot dry matter (g/pot)					
ICPL 227	6.20	6 dS/m	2.11 (34)	2.77 (45)	2.94 (47)	3.18 (51)	3.57 (58)	N.T
HY 3C	6.63	6 dS/m	1.79 (27)	2.07 (31)	2.12 (32)	2.35 (36)	2.40 (36)	
ICPL 227		8 dS/m	1.82 (29)	2.11 (34)	2.20 (35)	2.48 (39)	2.49 (40)	2.56 (41)
HY 3C		8 dS/m	0.87 (13)	1.19 (18)	1.28 (19)	1.41 (21)	1.46 (22)	1.53 (23)
SE ± 0.083			LSD at 5% = 0.235			CV% = 6.7		
			Root dry matter (g/pot)					
ICPL 227	2.79	6 dS/m	0.81 (29)	1.23 (44)	1.29 (46)	1.40 (50)	1.54 (55)	N.T
HY 3C	2.78	6 dS/m	0.57 (20)	0.86 (31)	0.88 (31)	0.89 (32)	0.90 (32)	
ICPL 227		8 dS/m	0.67 (24)	0.80 (29)	0.80 (29)	0.87 (31)	0.89 (32)	0.94 (34)
HY 3C		8 dS/m	0.27 (10)	0.32 (11)	0.34 (12)	0.42 (15)	0.45 (16)	0.51 (18)
SE ± 0.043			LSD at 5% = 0.122			CV% = 8.9		

Note: Figures in parenthesis are '% of control'
a. calcium/sodium at 6 dS/m : b. calcium/sodium at 8 dS/m
N.T - Not tested

4.3.2.1 Sodium: At 6 dS/m with 0.36mM calcium (Table 4.3.3.), leaf sodium (%) increased from 0.08% (control) to 0.895% in ICPL 227 and from 0.09% (control) to 2.30% in HY 3C. When substitution of calcium for sodium increased from 0.36 mM to 15 mM, leaf sodium decreased from 0.895% to 0.145% in ICPL 227 and from 2.30% to 0.39% in HY 3C. Leaf sodium in HY 3C was significantly higher than that in ICPL 227 at various calcium levels in the medium. At 8 dS/m with 0.36mM calcium, leaf sodium increased from 0.08% (control) to 2.25% in ICPL 227 and from 0.09% (control) to 4.65% in HY 3C. When substitution of calcium for sodium increased from 0.36 mM to 20 mM, leaf sodium decreased from 2.25% to 0.53% in ICPL 227 and from 4.65% to 2.30% in HY 3C. Leaf sodium was significantly higher in HY 3C compared to ICPL 227 at various calcium levels in the medium.

Stem sodium decreased with increasing calcium level at 6 and 8 dS/m, in both ICPL 227 and HY 3C. In HY 3C, stem sodium (%) was significantly higher than in ICPL 227 at various calcium levels at 6 and 8 dS/m salinity treatments and the trends were similar to those of leaf sodium levels.

At 6 dS/m with 0.36mM calcium, root sodium increased from 0.585% (control) to 2.63% in ICPL 227 and from 0.355% (control) to 2.11% in HY 3C. When substitution of calcium for sodium increased from 0.36 mM to 15 mM, root sodium decreased from 2.63% to 1.83% in ICPL 227 and from 2.11% to 1.65% in HY 3C. At 8 dS/m in the presence of 0.36 mM calcium, root sodium increased from 0.59% to 2.33% in ICPL 227 and from 0.36% to 1.50% in HY 3C. When substitution of calcium for sodium increased from 0.36 mM to 20 mM, root sodium (%) decreased from 2.33% to 1.80% in ICPL 227 and from 1.50% to 1.35% in HY 3C. However, in HY

Table 4.3.3. Effect of salinity with varying proportion of calcium and sodium on leaf, stem and root sodium (%) of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf sodium concentration (%)					
ICPL 227	0.08	6 dS/m	0.895	0.570	0.365	0.150	0.145	N.T
HY 3C	0.09	6 dS/m	2.300	1.730	1.470	0.780	0.390	
ICPL 227		8 dS/m	2.250	1.960	1.665	0.830	0.575	0.525
HY 3C		8 dS/m	4.650	4.190	3.205	3.100	2.650	2.300
SE ± 0.076			LSD at 5% = 0.224			CV% = 7.0		
			Stem sodium concentration (%)					
ICPL 227	0.05	6 dS/m	1.95	1.72	1.24	0.68	0.25	N.T
HY 3C	0.08	6 dS/m	2.38	2.10	1.65	0.95	0.55	
ICPL 227		8 dS/m	2.65	2.07	1.90	1.37	0.55	0.29
HY 3C		8 dS/m	3.75	3.13	3.03	2.60	2.30	2.15
SE ± 0.089			LSD at 5% = 0.26			CV% = 7.7		
			Root sodium concentration (%)					
ICPL 227	0.585	6 dS/m	2.63	1.94	1.93	1.85	1.83	N.T
HY 3C	0.355	6 dS/m	2.11	1.98	1.85	1.75	1.65	
ICPL 227		8 dS/m	2.33	2.05	1.90	1.80	1.80	1.80
HY 3C		8 dS/m	1.50	1.45	1.45	1.40	1.40	1.35
SE ± 0.102			LSD at 5% = 0.297			CV% = 8.5		

a. calcium/sodium at 6 dS/m; b. calcium/sodium at 8 dS/m
N.T - Not tested

3C, this decrease was not significant.

4.3.2.2 Potassium: At 6 dS/m with 0.36mM calcium, leaf potassium (%) decreased from 2.44% (control) to 2.09% in ICPL 227 and from 2.10 % (control) to 1.34% in HY 3C (Table 4.3.4.). When substitution of calcium for sodium increased from 0.36 mM to 15 mM in the medium, leaf potassium increased from 2.09% to 2.75% in ICPL 227 and from 1.34% to 2.13% in HY 3C. Leaf potassium levels were significantly higher in ICPL 227 than in HY 3C at each of the calcium levels in the medium. At 8 dS/m with 0.36mM calcium, leaf potassium decreased from 2.44% (control) to 1.48% in ICPL 227 and from 2.10% (control) to 0.87% in HY 3C. When substitution of calcium for sodium increased from 0.36 mM to 20 mM, leaf potassium increased from 1.48% to 2.43% in ICPL 227 and from 0.87% to 1.92% in HY 3C. Leaf potassium in ICPL 227 was significantly higher than in HY 3C at each calcium level in the medium.

Stem and root potassium also increased with increasing calcium level in the medium at both 6 and 8 dS/m salinity treatments in ICPL 227 and HY 3C (Table 4.3.4.). The trends were similar to the leaf potassium levels.

4.3.2.3 Potassium/sodium (K/Na) ratio: Leaf, stem and root K/Na at 6 and 8 dS/m are presented in Table 4.3.5. At 6 dS/m with 0.36mM calcium, leaf K/Na decreased from 31 (control) to 2.3 in ICPL 227 and from 25 (control) to 0.58 in HY 3C. When the substitution of calcium for sodium increased from 0.36 mM to 15 mM, leaf K/Na increased from 2.33 to 19 in ICPL 227 and from 0.58 to 5.5 in HY 3C. In ICPL 227,

Table 4.3.4. Effect of salinity with varying proportion of calcium and sodium on leaf, stem and root potassium (%) of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf potassium concentration (%)					
ICPL 227	2.44	6 dS/m	2.09	2.41	2.50	2.58	2.75	N.T
HY 3C	2.10	6 dS/m	1.34	1.57	1.62	1.70	2.13	
ICPL 227		8 dS/m	1.48	1.65	1.73	1.83	2.25	2.43
HY 3C		8 dS/m	0.87	1.04	1.19	1.50	1.76	1.92
SE ± 0.058			LSD at 5% = 0.171			CV% = 4.4		
			Stem potassium concentration (%)					
ICPL 227	1.535	6 dS/m	1.04	1.24	1.97	2.47	2.65	N.T
HY 3C	1.900	6 dS/m	1.23	1.35	1.65	2.17	2.55	
ICPL 227		8 dS/m	0.89	0.93	1.17	1.36	1.56	1.75
HY 3C		8 dS/m	0.90	1.03	1.21	1.39	1.41	1.46
SE ± 0.063			LSD at 5% = 0.184			CV% = 5.8		
			Root potassium concentration (%)					
ICPL 227	2.35	6 dS/m	1.55	1.65	2.10	2.25	2.55	N.T
HY 3C	2.25	6 dS/m	0.85	1.14	1.86	2.28	2.50	
ICPL 227		8 dS/m	1.49	1.65	1.85	2.06	2.05	2.25
HY 3C		8 dS/m	0.74	0.87	0.95	1.09	1.10	1.20
SE ± 0.051			LSD at 5% = 0.149			CV% = 4.3		

a. calcium/sodium at 6 dS/m; b. calcium/sodium at 8 dS/m
N.T - Not tested

Table 4.3.5. Effect of salinity with varying proportion of calcium and sodium on leaf, stem and root potassium/sodium (ratio) of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf potassium/sodium (ratio)					
ICPL 227	30.5	6 dS/m	2.33	4.23	6.85	17.23	19.00	N.T
HY 3C	24.7	6 dS/m	0.58	0.90	1.11	2.18	5.46	
ICPL 227		8 dS/m	0.66	0.84	1.04	2.20	3.92	4.63
HY 3C		8 dS/m	0.19	0.25	0.37	0.48	0.67	0.84
SE ± 0.27			LSD at 5% = 0.79				CV% = 6.9	
			Stem potassium/sodium (ratio)					
ICPL 227	32.0	6 dS/m	0.53	0.73	1.59	3.63	11.03	N.T
HY 3C	25.5	6 dS/m	0.51	0.64	1.00	2.29	4.68	
ICPL 227		8 dS/m	0.34	0.45	0.62	1.00	2.85	6.05
HY 3C		8 dS/m	0.24	0.33	0.40	0.54	0.61	0.68
SE ± 1.54			LSD at 5% = 4.51			CV% = 53.2		
			Root potassium/sodium (ratio)					
ICPL 227	4.07	6 dS/m	0.59	0.85	1.09	1.22	1.40	N.T
HY 3C	6.52	6 dS/m	0.41	0.58	1.00	1.30	1.52	
ICPL 227		8 dS/m	0.64	0.83	0.98	1.14	1.16	1.27
HY 3C		8 dS/m	0.50	0.60	0.66	0.78	0.79	0.90
SE ± 0.264			LSD at 5% = 0.772			CV% = 29.1		

a. calcium/sodium at 6 dS/m; b. calcium/sodium at 8 dS/m
N.T - Not tested

K/Na was significantly higher than in HY 3C at each calcium level. At 8 dS/m with 0.36mM calcium, leaf K/Na decreased from 31 (control) to 0.66 in ICPL 227 and from 25 (control) to 0.19 in HY 3C. When the substitution of calcium for sodium increased from 0.36 mM to 20 mM, leaf K/Na increased from 0.66 to 4.6 in ICPL 227 and from 0.19 to 0.84 in HY 3C. Leaf K/Na in ICPL 227 was significantly higher than in HY 3C at each calcium level. Stem and root K/Na increased with increasing calcium level in the medium in ICPL 227 and HY 3C at 6 and 8 dS/m and the trends were similar to that of leaf K/Na.

4.3.2.4 Calcium: The leaf calcium concentration of pigeonpea decreased from 1.92% (control) to 1.70 in ICPL 227 and from 1.89% to 1.06% in HY 3C at 6 dS/m with 0.36mM calcium (Table 4.3.6). However, in ICPL 227 this decrease was not significant. When the substitution of calcium for sodium increased from 0.36 mM to 15 mM, leaf calcium increased from 1.70% to 3.10% in ICPL 227 and from 1.06 to 3.45% in HY 3C. At 8 dS/m with 0.36mM calcium, leaf calcium decreased from 1.92% (control) to 1.37 in ICPL 227 and from 1.89% (control) to 0.87% in HY 3C. When the substitution of calcium for sodium increased from 0.36 mM to 20 mM, leaf calcium increased from 1.37% to 3.70% in ICPL 227 and from 0.87% to 4.70% in HY 3C. The stem and root calcium decreased at 6 and 8 dS/m at 0.36mM calcium level and increased with increasing calcium levels in the medium. The trends were similar to those of leaf calcium.

4.3.2.5 Chloride: At 6 dS/m with 0.36 mM calcium, leaf chloride concentration increased from 0.09% (control) to 2.05% in ICPL 227 and from 0.10% (control) to 2.79% in HY 3C (Table 4.3.7). When the

Table 4.3.6. Effect of salinity with varying proportion of calcium and sodium on leaf, stem and root calcium (%) of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf calcium concentration (%)					
ICPL 227	1.92	6 dS/m	1.70	1.76	2.49	2.67	3.10	N.T
HY 3C	1.89	6 dS/m	1.06	1.35	2.07	3.15	3.45	
ICPL 227		8 dS/m	1.37	1.70	2.45	3.15	3.35	3.70
HY 3C		8 dS/m	0.87	1.45	2.00	2.70	3.65	4.70
SE ± 0.11			LSD at 5% = 0.295			CV% = 5.9		
			Stem calcium concentration (%)					
ICPL 227	1.55	6 dS/m	1.05	1.14	1.41	1.65	1.75	N.T
HY 3C	1.75	6 dS/m	1.10	1.30	1.85	2.20	2.55	
ICPL 227		8 dS/m	1.06	1.12	1.40	1.90	2.05	2.35
HY 3C		8 dS/m	1.10	1.25	1.70	2.10	2.20	2.35
SE ± 0.087			LSD at 5% = 0.254			CV% = 7.4		
			Root calcium concentration (%)					
ICPL 227	0.80	6 dS/m	0.70	0.80	0.80	0.80	0.80	N.T
HY 3C	0.80	6 dS/m	0.40	0.55	0.65	0.70	0.75	
ICPL 227		8 dS/m	0.60	0.65	0.70	0.70	0.75	0.80
HY 3C		8 dS/m	0.40	0.48	0.65	0.75	0.80	0.85
SE ± 0.067			LSD at 5% = 0.196			CV% = 13.5		

a. calcium/sodium at 6 dS/m; b. calcium/sodium at 8 dS/m
N.T - Not tested

Table 4.3.7. Effect of salinity with varying proportion of calcium and sodium on leaf, stem and root chloride (%) of pigeonpea genotypes ICPL 227 (tolerant) and HY 3C (sensitive).

Genotype	Control	Salinity level	Calcium/sodium content (mM) a 0.36/59.3 b 0.36/79.3	1/58 1/78	5/50 5/70	10/40 10/60	15/30 15/50	20/40
			Leaf chloride concentration (%)					
ICPL 227	0.09	6 dS/m	2.05	2.08	2.45	2.55	2.65	N.T
HY 3C	0.10	6 dS/m	2.79	3.18	3.55	3.85	4.15	
ICPL 227		8 dS/m	2.35	2.65	3.55	3.75	4.05	4.05
HY 3C		8 dS/m	3.45	3.75	4.40	5.10	5.65	6.25
SE ± 0.077			LSD at 5% = 0.226			CV% = 3.3		
			Stem chloride concentration (%)					
ICPL 227	0.145	6 dS/m	1.94	2.06	2.13	2.10	2.15	N.T
HY 3C	0.225	6 dS/m	2.05	2.35	2.43	2.45	2.55	
ICPL 227		8 dS/m	2.13	2.35	2.45	2.60	2.75	2.75
HY 3C		8 dS/m	3.18	3.40	3.50	3.75	3.95	4.15
SE ± 0.046			LSD at 5% = 0.135			CV% = 2.6		
			Root chloride concentration (%)					
ICPL 227	0.79	6 dS/m	1.64	2.05	2.15	2.10	2.15	N.T
HY 3C	0.56	6 dS/m	1.23	1.75	1.95	2.05	2.04	
ICPL 227		8 dS/m	1.85	2.15	2.05	2.15	2.20	2.20
HY 3C		8 dS/m	1.52	1.70	1.75	1.95	2.05	2.10
SE ± 0.084			LSD at 5% = 0.246			CV% = 6.5		

a. calcium/sodium at 6 dS/m; b. calcium/sodium at 8 dS/m
N.T - Not tested

substitution of calcium for sodium increased from 0.36 mM to 15 mM, leaf chloride increased from 2.05% to 2.65% in ICPL 227 and from 2.79% to 4.15% in HY 3C. In ICPL 227, leaf chloride levels were significantly lower than in HY 3C at each calcium level in the medium. At 8 dS/m with 0.36mM calcium, leaf chloride increased from 0.09% (control) to 2.35% in ICPL 227 and from 0.10% (control) to 3.45% in HY 3C. When the substitution of calcium for sodium increased from 0.36 mM to 20 mM, leaf chloride (%) increased from 2.35% to 4.05% in ICPL 227 and from 3.45% to 6.25% in HY 3C. Leaf chloride in HY 3C was significantly higher than in ICPL 227 at each calcium level. The trends in stem chloride (%) at 6 and 8 dS/m at different calcium levels were similar to that of leaf chloride. The increase in root chloride with increasing calcium level in the medium at 6 and 8 dS/m in ICPL 227 and HY 3C was relatively less compared to that of leaf chloride.

4.4 Response of wild relatives of pigeonpea to salinity - ionic relations and their relevance to physiological basis of tolerance.

This investigation was aimed at assessing the salinity tolerance in the wild relatives of pigeonpea and understanding their ion regulation behaviour in comparison with the cultivated pigeonpeas. Four wild species related to pigeonpea, namely Atylosia platycarpa, A. scarabaeoides, Rynchosia albiflora, Dunbaria ferruginea, and two cultivated pigeonpea genotypes ICPL 227 (most tolerant) and HY 3C (least tolerant) were selected for this study. The sand culture system was used to grow the plants. The experiment was laid as a randomized complete block and replicated four times. There were 5 salinity treatments: 0, 4, 6, 8 and 10 dS/m. Plants were harvested 55 days after sowing.

Findings

Within a week after imposing salinity treatments, salt burning symptoms appeared on the primary leaves of R. albiflora at 6 dS/m and higher salinity levels. In HY 3C and D. ferruginea, such symptoms appeared at 8 dS/m and higher salinity levels and in ICPL 227, such symptoms appeared at 10 dS/m. In A. platycarpa, symptoms were not apparent at any of the salinity levels.

By 50 days, these symptoms had spread to the trifoliate leaves in several cases. R. albiflora was able to survive only at 4 dS/m, with salt burn symptoms on a majority of the plants. At 6 dS/m, most of the plants died and at 8 and 10dS/m, none of the plants of this species survived. In D. ferruginea, A. scarabaeoides and HY 3C

(Plate 2b), plants were healthy without salt burning symptoms at 4 dS/m. Plants were able to survive at 6 and 8 dS/m with salt burning symptoms. In HY 3C and D. ferruginea, these symptoms were severe on a majority of the plants resulting in plant mortality at 8 dS/m. At 10 dS/m, none of these three species survived. In ICPL 227 (Plate 2a), salt burning symptoms appeared only at 8 and 10 dS/m. These symptoms became severe and wilting symptoms appeared in a majority of the plants with no plants surviving after 50 days. A. platycarpa was the only species that could grow and set pods up to 10 dS/m, without salt burning symptoms (Plate 3a and 3c).

4.4.1 Effects on leaf area: In all the species, leaf area was decreased with increasing salinity (Table 4.4.1 and Fig 4.4.1). However, such reduction was least in A. platycarpa at each salinity level in comparison with the other species. ICPL 227 had significantly higher leaf area than HY 3C at various salinity levels. The reduction in leaf area in D. ferruginea and A. scarabaeoides was similar to that of ICPL 227 at 4 dS/m but significantly higher at 6 and 8 dS/m. At 10 dS/m, A. platycarpa was the only species surviving and its leaf area was about 54% of the control.

4.4.2 Effects on shoot and root dry matter: In all the species shoot dry matter was reduced with increasing salinity (Table 4.4.1 and Fig. 4.4.1). However, the reduction was least in A. platycarpa at each salinity level, and greatest for R. albiflora. In ICPL 227, such reduction was significantly less than HY 3C at each salinity level. At 10 dS/m, A. platycarpa was the only species able to produce shoot dry matter about 50% of its control. Root dry matter decreased with

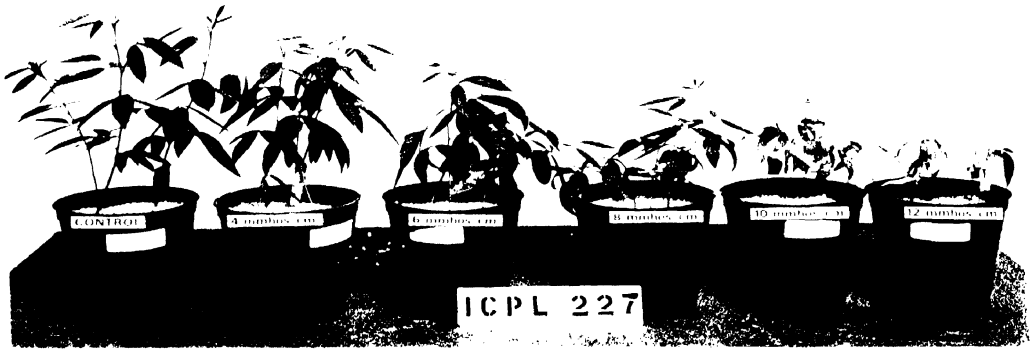

Plate 2a. Growth response of ICPL 227 to different levels of salinity, 55 days after sowing.

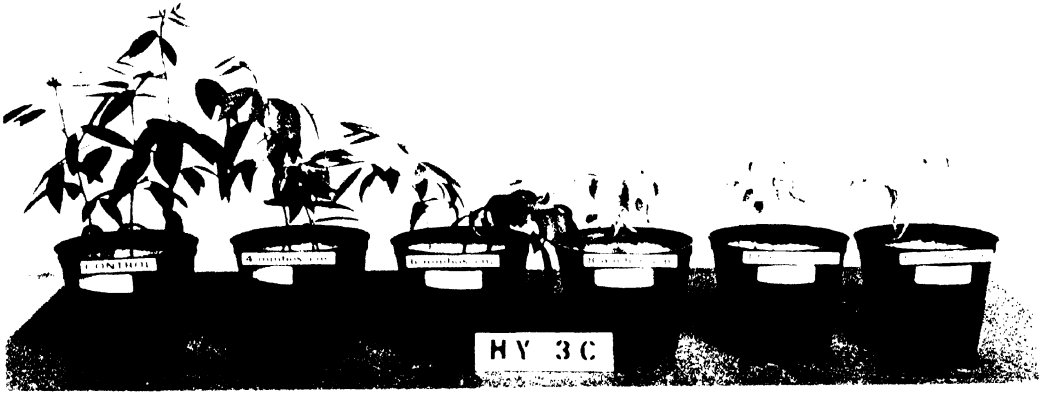

Plate 2b. Growth response of HY 3C to different levels of salinity, 55 days after sowing.

Plate 3a. Growth response of Atylosia platycarpa to different levels of salinity, 55 days after sowing.

Plate 3b. Growth response of Atylosia acutifolia to different levels of salinity, 55 days after sowing.

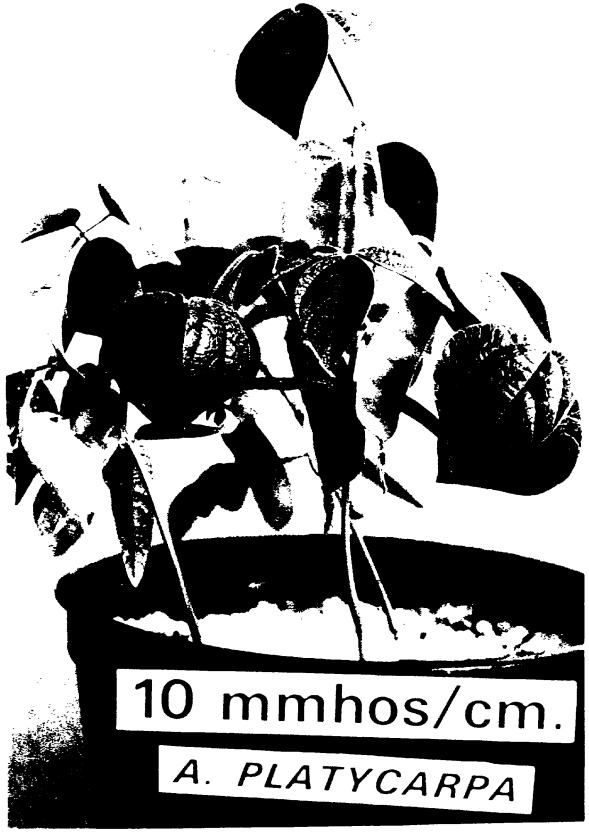

Plate 3c. Growth and podding of Atylosia platycarpa at 10 dS/m salinity level, 55 days after sowing.

Table 4.4.1. Effect, of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf area, shoot and root dry matter.

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
			Leaf area (cm2/pot)		
A. platycarpa	853	709 (83)	640 (76)	511 (60)	452 (54)
A. scarabaeoides	157	119 (76)	79 (50)	33 (22)	d
R. albiflora	123	37 (30)	27 (22)b	d	d
D. ferruginea	125	91 (73)	47 (40)	d	d
ICPL 227	506	362 (72)	303 (60)	202 (40)	d
HY 3C	539	354 (66)	178 (34)	d	d
SE ± 17.14		LSD at 5% = 48.5		CV% = 15.7	
SE ± 2.87 (% of control)		LSD at 5% = 8.12		CV% = 11.6	
d. Plants are died					
			Shoot dry matter (g/pot)		
A. platycarpa	16.25	13.17 (81)	12.35 (76)	10.08 (62)	8.45 (52)
A. scarabaeoides	1.09	0.77 (71)	0.56 (51)	0.30 (28)	0.11 (10)
R. albiflora	0.73	0.19 (26)	0.15 (21)	0.08 (12)	0.07 (9)
D. ferruginea	0.76	0.53 (70)	0.32 (42)	0.24 (31)	0.06 (8)
ICPL 227	4.11	2.88 (70)	2.47 (61)	1.64 (41)	0.41 (9)
HY 3C	4.11	2.30 (51)	1.23 (30)	0.65 (16)	0.21 (5)
SE ± 0.117		LSD at 5% = 0.332		CV% = 8.2	
SE ± 2.12 (for % of control)		LSD at 5% = 5.97		CV% = 8.3	
			Root dry matter (mg/pot)		
A. platycarpa	2269	1917 (85)	1679 (75)	1361 (61)	1135 (50)
A. scarabaeoides	252	177 (70)	116 (46)	116 (23)	24 (10)
R. albiflora	226	57 (25)	34 (15)	16 (8)	10 (4)
D. ferruginea	153	111 (73)	59 (40)	38 (25)	10 (5)
ICPL 227	1308	903 (69)	706 (55)	510 (39)	135 (10)
HY 3C	1466	779 (53)	469 (32)	196 (13)	108 (8)
SE ± 34		LSD at 5% = 97.4		CV% = 12.7	
SE ± 3.79 (for % of control)		LSD at 5% = 10.7		CV% = 15.2	

Note: Figures in parenthesis are ' % of control'

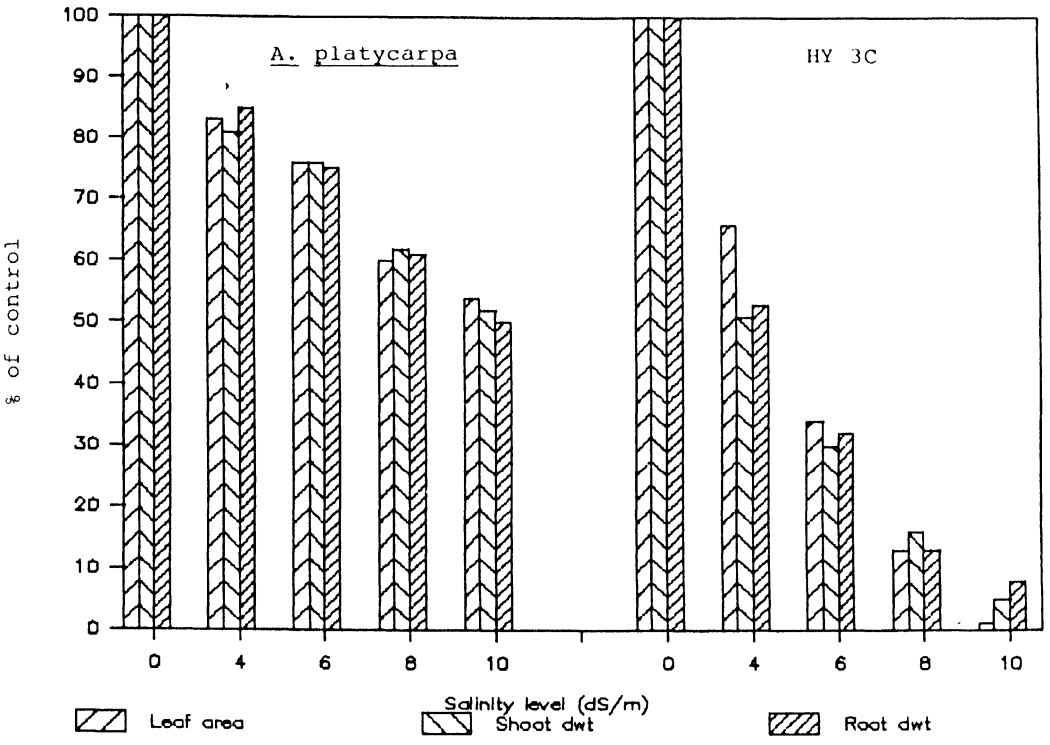

Fig. 4.4.1. Effect of salinity on plant growth of A. platycarpa (tolerant) and HY3C (sensitive).

increasing salinity in the medium and the trends were similar to the shoot dry matter response.

4.4.3 Ionic relations

4.4.3.1 Sodium: In all the species, leaf sodium increased with increasing salinity in the medium (Table 4.4.2 and Fig. 4.4.2). In R. albiflora, such an increase was significant at 4 dS/m and above. In D. ferruginea, A. scarabaeoides and HY 3C, leaf sodium levels increased significantly only at 6 dS/m and above, whereas in ICPL 227, the increase was significant only at 8 dS/m and above. In A. platycarpa, the increase in leaf sodium level was significant only at 10 dS/m. In A. platycarpa, leaf sodium was the lowest at various salinity levels, compared to the other species. At 4 and 6 dS/m, the differences in leaf sodium between A. platycarpa and ICPL 227 were not significant. At 8 dS/m, leaf sodium in A. platycarpa, A. scarabaeoides and ICPL 227, was significantly lower than in D. ferruginea, R. albiflora, and HY 3C. At 10 dS/m, A. platycarpa was the only species that maintained a low leaf sodium (0.29%), whereas in the other species which failed to survive at this salinity level, the leaf sodium levels ranged from 1.25% to 2.90%.

Stem sodium (%) also increased with increasing salinity and the trends were similar to those of leaf sodium (Table 4.4.2 and Fig. 4.4.2). Root sodium (%) was significantly affected with increasing salinity (Table 4.4.2 and Fig. 4.4.2). In all the species, root sodium (%) increased with salinity. However, such an increase was only up to 6 dS/m in A. scarabaeoides, D. ferruginea, and HY 3C

Table 4.4.2. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root sodium concentration (%)

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
			Leaf sodium concentration (%)		
A. platycarpa	0.12	0.16	0.18	0.21	0.29
A. scarabaeoides	0.16	0.24	0.30	0.59	1.25
R. albiflora	0.19	0.41	0.56	1.34	1.94
D. ferruginea	0.17	0.25	0.92	1.20	2.27
ICPL 227	0.15	0.16	0.21	0.55	1.33
HY 3C	0.16	0.21	0.38	2.15	2.90
SE ± 0.047		LSD at 5% = 0.135			CV% = 9.5
			Stem sodium concentration (%)		
A. platycarpa	0.07	0.24	0.32	0.51	0.58
A. scarabaeoides	0.24	0.34	0.53	0.88	2.31
R. albiflora	0.20	0.43	0.65	1.50	2.25
D. ferruginea	0.17	0.47	0.94	1.95	2.45
ICPL 227	0.21	0.25	0.31	0.32	2.88
HY 3C	0.21	0.29	0.38	2.32	3.36
SE ± 0.08		LSD at 5% = 0.238			CV% = 12.7
			Root sodium concentration (%)		
A. platycarpa	0.91	2.29	2.33	2.53	2.53
A. scarabaeoides	0.60	0.76	0.82	0.81	0.76
R. albiflora	0.47	1.14	1.39	1.35	1.20
D. ferruginea	0.85	1.74	2.20	1.80	1.45
ICPL 227	0.60	1.50	1.54	1.57	1.27
HY 3C	0.50	1.48	1.55	1.04	1.00
SE ± 0.085		LSD at 5% = 0.244			CV% = 9.0

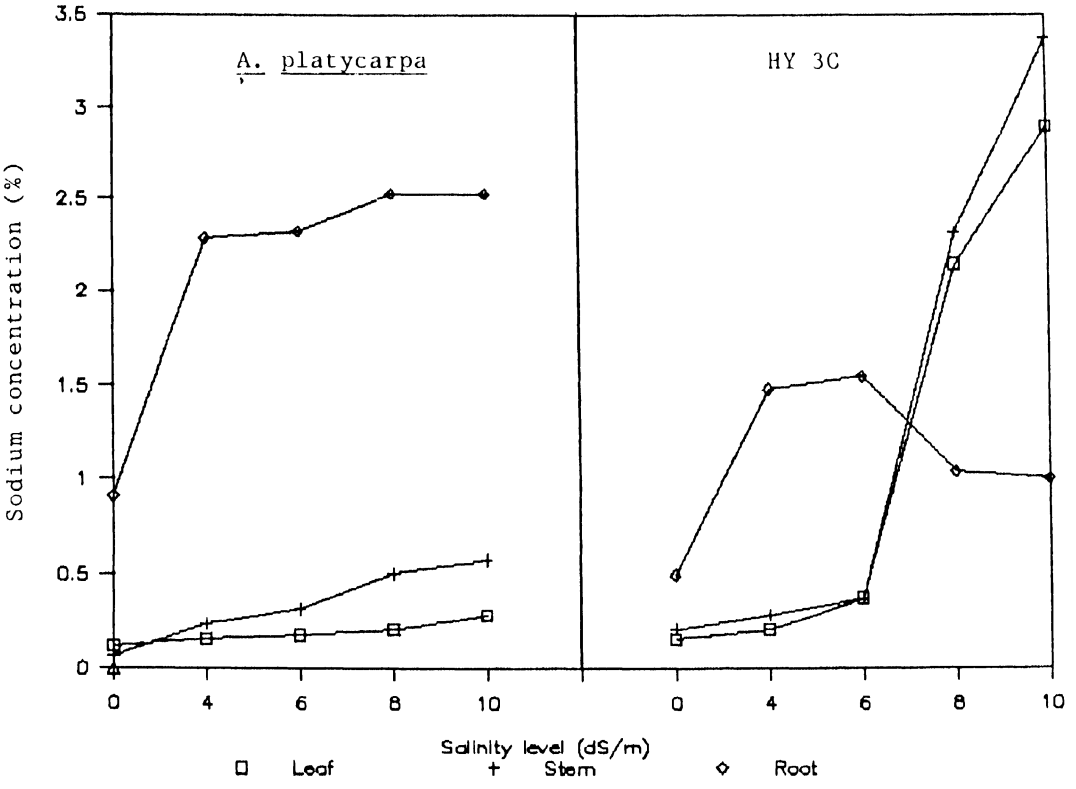

Fig. 4.4.2. Effect of salinity on tissue sodium concentration (%) of A. platycarpa (tolerant) and HY 3C (sensitive).

and then there was a decline at higher levels of salinity. In ICPL 227, the increase was only up to 8 dS/m while in A. platycarpa, root sodium (%) levels increased with salinity up to 10 dS/m.

4.4.3.2 Potassium: In the most tolerant species (A. platycarpa) leaf potassium levels increased with increasing salinity up to 10 dS/m (>63% increase over the control at 10 dS/m) (Table 4.4.3 and Fig 4.4.3). In ICPL 227, potassium levels increased only up to 6 dS/m and then declined at 8 and 10 dS/m. In A. scarabaeoides, R. albiflora, D. ferruginea and HY 3C, leaf potassium decreased with increasing salinity, and at 8 and 10 dS/m this reduction was most severe; i.e the leaf potassium was reduced to 37% of control in D. ferruginea and to 64% of control in R. albiflora.

Stem potassium levels increased with increasing salinity in A. platycarpa, and at 10 dS/m there was a 41% increase over its the control (Table 4.4.3 and Fig 4.4.3). In ICPL 227 and HY 3C, stem potassium levels increased up to 6 dS/m and then declined at 8 and 10 dS/m salinity levels; such a decline was more severe in HY 3C than in ICPL 227. In A. scarabaeoides, R. albiflora, and D. ferruginea, stem potassium levels decreased with increasing salinity in the medium and the decrease was significantly higher in R. albiflora and D. ferruginea than in A. scarabaeoides. At 10 dS/m, where A. platycarpa was the only species able to maintain higher potassium levels than its control, all the remaining species failed to survive at this level and suffered a decrease in potassium from 40% to 70% compared to their respective controls.

Table 4.4.3. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root potassium (%) concentration.

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
			Leaf potassium concentration (%)		
A. platycarpa	0.46	0.68 (148)	0.77 (167)	0.75 (163)	0.75 (163)
A. scarabaeoides	2.34	2.31 (99)	2.24 (96)	1.69 (72)	1.40 (60)
R. albiflora	2.95	2.30 (78)	2.10 (71)	1.90 (64)	1.90 (64)
D. ferruginea	2.87	2.57 (90)	1.90 (66)	1.32 (46)	1.05 (37)
ICPL 227	2.15	2.42 (113)	2.71 (126)	2.15 (100)	1.92 (89)
HY 3C	2.20	2.18 (99)	2.14 (97)	1.65 (75)	1.15 (52)
SE ± 0.09		LSD at 5% = 0.26		CV% = 7.0	
			Stem potassium concentration (%)		
A. platycarpa	1.23	1.47 (120)	1.61 (131)	1.58 (128)	1.73 (141)
A. scarabaeoides	2.35	2.32 (99)	2.02 (86)	1.78 (76)	1.52 (65)
R. albiflora	2.70	2.05 (76)	1.80 (67)	1.60 (59)	1.40 (52)
D. ferruginea	2.94	2.45 (83)	1.90 (65)	1.15 (39)	0.90 (31)
ICPL 227	1.70	2.56 (151)	2.60 (153)	1.67 (98)	1.01 (59)
HY 3C	1.94	2.41 (124)	2.16 (111)	1.05 (54)	0.85 (44)
SE ± 0.075		LSD at 5% = 0.215		CV% = 5.8	
			Root potassium concentration (%)		
A. platycarpa	1.39	1.67 (120)	1.68 (121)	1.68 (121)	1.80 (129)
A. scarabaeoides	2.72	2.38 (88)	1.51 (56)	0.95 (35)	0.55 (20)
R. albiflora	3.35	2.35 (70)	1.70 (51)	0.85 (25)	0.60 (18)
D. ferruginea	3.70	2.85 (77)	1.85 (50)	1.03 (28)	0.66 (18)
ICPL 227	2.28	2.60 (114)	2.70 (118)	2.25 (99)	1.05 (46)
HY 3C	2.30	2.45 (107)	2.60 (113)	0.85 (37)	0.60 (26)
SE ± 0.114		LSD at 5% = 0.329		CV% = 8.8	

Note: Figures in parenthesis are '% of control'

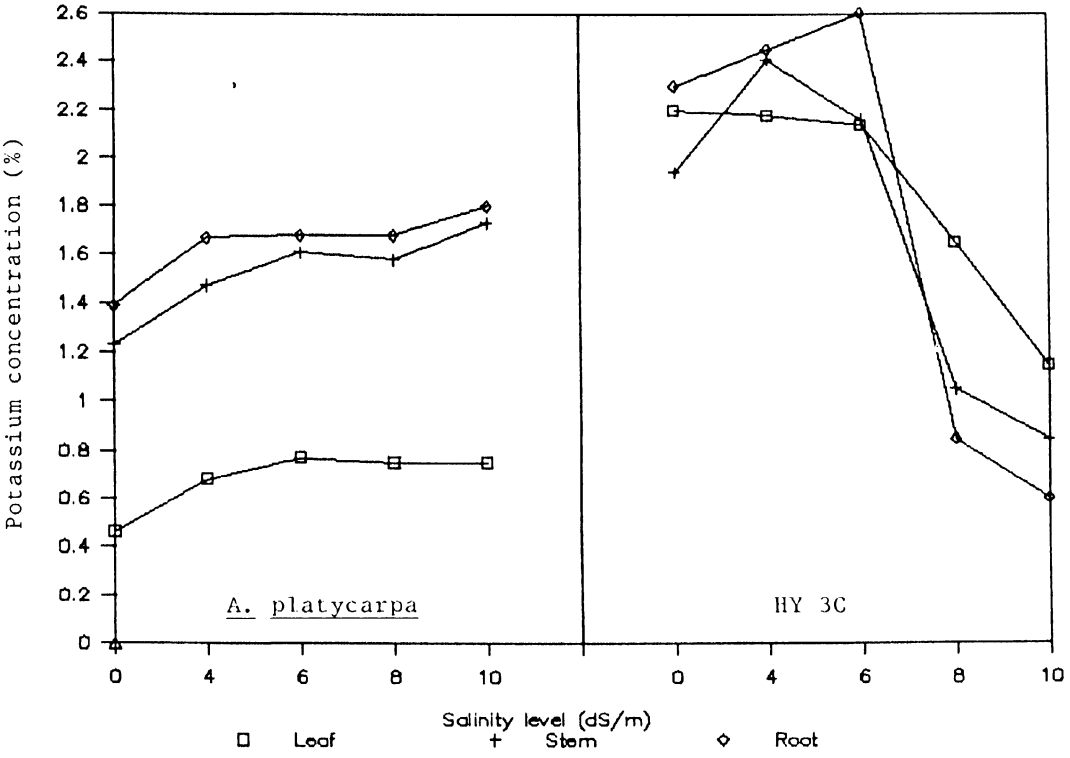

Fig. 4.4.3. Effect of salinity on tissue potassium concentration (%) of A. platycarpa (tolerant) and HY 3C (sensitive).

As for stem potassium, in A. platycarpa root potassium increased with increasing salinity in the medium and a 29% increase was observed at 10 dS/m (Table 4.4.3 and Fig 4.4.3). In ICPL 227, root potassium increased up to 6 ds/m and then declined to about the control level. In HY 3C, there was an increase in root potassium up to 6 dS/m, but at 8 and 10 dS/m salinity levels there was a sharp decrease (70 to 80%), where this genotype failed to survive. In other species namely, A. scarabaeoides, R. albiflora and D. ferruginea, root potassium decreased with increasing salinity and at 10 dS/m, where these species failed to survive, the decrease was as much as 80%.

4.4.3.3 Potassium/sodium ratio (K/Na): Leaf K/Na was not significantly affected in A. platycarpa at various salinity levels (Table 4.4.4). In ICPL 227, up to 6 dS/m there was no significant change in K/Na, but at 8 and 10 dS/m it decreased to 27% and 10% of its control, respectively. In A. scarabaeoides, R. albiflora, D. ferruginea and HY 3C, leaf K/Na decreased with increasing salinity and at 8 and 10 dS/m, there was a reduction up to 80% - 90%. Stem and root K/Na (ratio) decreased significantly in all the species (Table 4.4.4) with increasing salinity. However, such reduction was less in A. platycarpa and ICPL 227 at the various salinity levels.

4.4.3.4 Calcium: In all the species leaf calcium (%) increased with increasing salinity with a significant interaction between species and salinity treatment (Table 4.4.5). The increase was significantly higher in HY 3C at all salinity levels. Stem and root calcium (%) increased with increasing salinity (Table 4.4.5). In all the species, stem and root calcium (%) increased with increasing salinity in the

Table 4.4.4. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root potassium/sodium ratio.

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
			Leaf potassium/sodium ratio		
A. platycarpa	3.80	4.29 (113)	4.25 (112)	3.57 (94)	2.58 (68)
A. scarabaeoides	14.60	9.96 (68)	7.57 (52)	3.00 (21)	1.13 (8)
R. albiflora	15.53	5.70 (37)	3.78 (24)	1.42 (9)	0.98 (6)
D. ferruginea	17.37	10.28 (59)	2.06 (12)	1.11 (6)	0.46 (3)
ICPL 227	14.42	15.19 (105)	13.03 (90)	3.96 (27)	1.44 (10)
HY 3C	14.23	10.45 (73)	5.64 (40)	0.77 (5)	0.40 (3)
SE ± 0.689		LSD at 5% = 1.99		CV% = 15.1	
			Stem potassium/sodium ratio		
A. platycarpa	19.06	6.64 (35)	5.24 (27)	3.11 (16)	2.98 (16)
A. scarabaeoides	9.78	6.83 (70)	3.84 (39)	2.04 (21)	0.66 (7)
R. albiflora	13.56	4.78 (35)	2.80 (21)	1.08 (8)	0.65 (5)
D. ferruginea	17.32	5.27 (30)	2.02 (12)	0.60 (3)	0.37 (2)
ICPL 227	8.09	10.44 (129)	8.38 (104)	5.21 (64)	0.35 (4)
HY 3C	9.24	8.31 (90)	5.68 (61)	0.45 (5)	0.25 (3)
SE ± 0.595		LSD at 5% = 1.72		CV% = 15.3	
			Root potassium/sodium ratio		
A. platycarpa	1.53	0.73 (48)	0.72 (47)	0.67 (44)	0.71 (46)
A. scarabaeoides	4.57	3.15 (69)	1.85 (40)	1.17 (26)	0.72 (16)
R. albiflora	7.13	2.06 (29)	1.23 (17)	0.64 (9)	0.50 (7)
D. ferruginea	4.39	1.64 (37)	0.86 (20)	0.58 (13)	0.45 (10)
ICPL 227	3.81	1.76 (46)	1.76 (46)	1.43 (38)	0.83 (22)
HY 3C	4.88	1.66 (34)	1.69 (35)	0.83 (17)	0.62 (13)
SE ± 0.270		LSD at 5% = 0.78		CV% = 21.0	

Note: Figures in parenthesis are '% of control'

Table 4.4.5. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root calcium concentration (%).

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
			Leaf calcium concentration (%)		
A. platycarpa	2.19	2.68	2.86	2.90	3.14
A. scarabaeoides	1.43	2.15	2.23	2.30	2.50
R. albiflora	1.55	1.75	2.43	2.72	3.05
D. ferruginea	1.77	2.35	2.35	2.77	3.05
ICPL 227	1.90	2.28	2.90	3.35	3.97
HY 3C	1.90	3.33	3.72	4.85	6.00
SE ± 0.126		LSD at 5% = 0.365			CV% = 6.5
			Stem calcium concentration (%)		
A. platycarpa	2.09	2.50	2.95	3.10	3.35
A. scarabaeoides	1.45	1.50	1.70	1.90	2.05
R. albiflora	1.30	1.75	2.25	2.35	3.50
D. ferruginea	1.40	2.35	2.55	2.90	3.10
ICPL 227	1.51	1.67	1.70	2.37	2.62
HY 3C	1.49	1.80	2.70	2.90	4.00
SE ± 0.141		LSD at 5% = 0.408			CV% = 8.7
			Root calcium concentration (%)		
A. platycarpa	0.68	0.79	0.83	0.89	0.91
A. scarabaeoides	0.84	1.08	1.23	1.46	1.84
R. albiflora	0.74	1.40	1.65	1.90	2.20
D. ferruginea	1.11	1.29	1.46	1.60	1.74
ICPL 227	0.85	0.88	0.95	0.90	1.45
HY 3C	0.77	0.79	0.85	0.90	2.08
SE ± 0.089		LSD at 5% = 0.257			CV% = 10.5

medium with a significant interaction between species and salinity treatment.

4.4.3.5 Magnesium: In A. platycarpa, there was no significant change in the leaf magnesium with increasing salinity (Table 4.4.6), whereas in all the other five species/genotypes (A. scarabaeoides, R. albiflora, D. ferruginea, ICPL 227, and HY 3C) leaf magnesium (%) decreased with increasing salinity and at 10 dS/m the decrease was as much as 70%. Stem magnesium (%) also decreased with increasing salinity (Table 4.4.6). The interaction between species and salinity treatment in the stem magnesium levels was significant. In A. platycarpa, increasing salinity did not have any significant effect on the stem magnesium levels. In A. scarabaeoides, R. albiflora, D. ferruginea, stem magnesium (%) decreased, whereas in ICPL 227 and HY 3C stem magnesium (%) increased with increasing salinity in the medium.

Root magnesium (%) was increased with increasing salinity in A. platycarpa. In D. ferruginea, ICPL 227 and HY 3C, root magnesium (%) levels decreased with increasing salinity, whereas in A. scarabaeoides and R. albiflora, there was no significant change.

4.4.3.6 Chloride: In all the species, leaf chloride (%) increased with increasing salinity (Table 4.4.7 and Fig 4.4.4). In A. platycarpa, this increase was significant only up to 6 dS/m and there was no significant increase thereafter, whereas in the other species (A. scarabaeoides, R. albiflora, D. ferruginea, ICPL 227 and HY 3C) the increase was significant at every salinity level. In ICPL 227 at

Table 4.4.6. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root magnesium concentration (%).

Species/genotype	Salinity level (dS/m)				
	0	4	6	8	10
	Leaf magnesium concentration (%)				
A. platycarpa	0.39	0.40	0.39	0.39	0.39
A. scarabaeoides	0.36	0.23	0.14	0.12	0.10
R. albiflora	0.30	0.20	0.18	0.17	0.14
D. ferruginea	0.36	0.29	0.29	0.27	0.22
ICPL 227	0.24	0.21	0.19	0.15	0.14
HY 3C	0.33	0.26	0.25	0.22	0.19
SE ± 0.018	LSD at 5% = 0.052			CV% = 10.2	
	Stem magnesium concentration (%)				
A. platycarpa	0.22	0.21	0.21	0.22	0.22
A. scarabaeoides	0.51	0.31	0.19	0.17	0.17
R. albiflora	0.35	0.19	0.14	0.13	0.12
D. ferruginea	0.35	0.25	0.20	0.20	0.20
ICPL 227	0.10	0.16	0.16	0.17	0.18
HY 3C	0.12	0.14	0.21	0.23	0.24
SE ± 0.028	LSD at 5% = 0.079			CV% = 18.6	
	Root magnesium concentration (%)				
A. platycarpa	0.66	0.67	0.77	0.85	0.85
A. scarabaeoides	0.43	0.44	0.46	0.45	0.46
R. albiflora	0.48	0.55	0.54	0.54	0.54
D. ferruginea	0.51	0.49	0.49	0.38	0.34
ICPL 227	0.70	0.69	0.65	0.60	0.51
HY 3C	0.66	0.64	0.53	0.41	0.33
SE ± 0.038	LSD at 5% = 0.11			CV% = 9.7	

Table 4.4.7. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf, stem and root chloride concentration (%).

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
		Leaf chloride concentration (%)			
A. platycarpa	0.10	2.50	3.58	3.59	3.84
A. scarabaeoides	0.13	1.11	2.17	3.13	4.00
R. albiflora	0.15	3.29	3.57	3.90	4.35
D. ferruginea	0.09	1.71	2.90	4.10	4.40
ICPL 227	0.15	2.10	2.50	3.80	6.33
HY 3C	0.15	2.55	3.85	6.01	7.85
SE ± 0.161		LSD at 5% = 0.466		CV% = 7.8	
		Stem chloride concentration (%)			
A. platycarpa	0.15	1.39	1.69	1.80	2.19
A. scarabaeoides	0.30	1.38	1.89	2.23	2.55
R. albiflora	0.13	4.10	4.55	5.25	5.65
D. ferruginea	0.11	1.90	3.40	4.55	5.25
ICPL 227	0.15	1.60	2.40	2.52	3.99
HY 3C	0.31	1.65	2.16	3.71	7.40
SE ± 0.139		LSD at 5% = 0.4		CV% = 7.7	
		Root chloride concentration (%)			
A. platycarpa	0.45	2.95	3.10	3.23	3.24
A. scarabaeoides	0.45	0.90	0.97	3.44	3.55
R. albiflora	0.55	0.85	1.25	2.10	2.10
D. ferruginea	0.50	1.10	1.25	2.65	2.75
ICPL 227	0.82	2.10	2.25	2.25	2.89
HY 3C	0.75	2.14	2.40	1.53	1.25
SE ± 0.099		LSD at 5% = 0.286		CV% = 7.5	

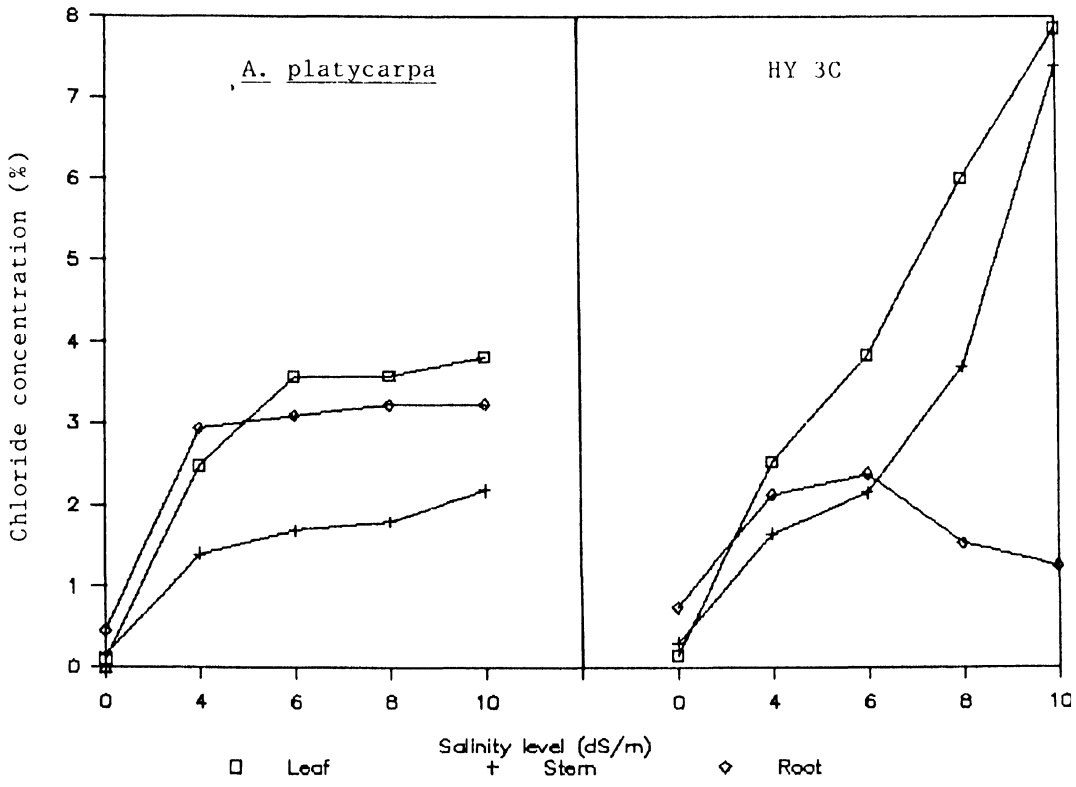

Fig. 4.4.4. Effect of salinity on tissue chloride concentration (%) of A. platycarpa (tolerant) and HY 3C (sensitive).

10 dS/m and in HY 3C at 8 and 10 dS/m, leaf chloride increased to very high concentrations (6 to 8%). Stem chloride (%) also increased with salinity and the interaction between salinity treatment and species was significant (Table 4.4.7) The stem chloride at various salinity levels were significantly lower in A. platycarpa than in other species. Root chloride (%) also increased with increasing salinity in the medium and the increase was significantly higher in A. platycarpa than in other species (Table 4.4.7).

4.4.3.7 Manganese: The manganese levels in leaf were increased with incrasing salinity in A. platycarpa, D. ferruginea, ICPL 227 and HY 3C, while in A. scarabaeoides and R. albiflora, it was decreased (Table 4.4.8).

4.4.3.8 Zinc: In all the species, zinc levels in leaf were increased with increasing salinity (Table 4.4.8).

4.4.3.9 Iron: In A. platycarpa, there was no significant change in leaf iron content with increasing salinity while in R. albiflora, leaf and stem iron levels increased with increasing salinity (Table 4.4.7). whereas in A. scarabaeoides, D. ferruginea, ICPL 227, and HY 3C, leaf iron levels decreased with increasing salinity (Table 4.4.8).

Table 4.4.8. Effect of salinity on wild relatives of pigeonpea, ICPL 227 and HY 3C in relation to leaf manganese, zinc and iron concentration (ppm).

Species/genotype	Salinity level (dS/m) 0	4	6	8	10
	Leaf manganese concentration (ppm)				
A. platycarpa	150	153	175	180	245
A. scarabaeoides	333	275	187	184	170
R. albiflora	159	145	137	121	115
D. ferruginea	108	118	125	135	145
ICPL 227	77	85	105	117	129
HY 3C	53	80	119	200	351
SE ± 8.8		LSD at 5% = 25.5		CV% = 8.0	
	Leaf zinc concentration (ppm)				
A. platycarpa	36	37	39	43	48
A. scarabaeoides	30	36	47	57	92
R. albiflora	46	51	58	66	74
D. ferruginea	27	31	36	48	55
ICPL 227	26	34	36	47	48
HY 3C	31	36	41	48	53
SE ± 3.92		LSD at 5% = 11.3		CV% = 12.3	
	Leaf iron concentration (ppm)				
A. platycarpa	201	171	154	152	150
A. scarabaeoides	947	766	749	623	600
R. albiflora	439	507	578	984	1175
D. ferruginea	775	670	597	590	595
ICPL 227	242	210	163	154	158
HY 3C	226	219	213	179	165
SE ± 24.67		LSD at 5% = 71.34		CV% = 7.8	

4.5 Variation for salinity tolerance among different species of Atylosia - ionic relations and its relevance to the physiological basis of tolerance.

This is essentially a continuation of the Experiment 4.4. The present investigation was aimed at assessing the variation Atylosia sp. to salinity tolerance and to understand the ionic relations and its relevance in the physiological mechanism of tolerance to salinity.

Ten species of Atylosia namely, (1) A. albicans, (2) A. acutifolia, (3) A. cajanifolia, (4) A. goensis, (5) A. grandifolia, (6) A. lineata, (7) A. lanceolata, (8) A reticulata, (9) A. sericea, and (10) A. volubilis, were selected for this study. The sand culture system was used to grow the plants and the experiment was laid out as a randomized complete block design with 4 replications. There were five salinity levels: 0, 4, 6, 8 and 10 dS/m. Plants were harvested 55 days after sowing.

Findings

Within ten days after imposing salt treatments, salt burning symptoms appeared in some species. They were confined to primary leaves initially and then spread to trifoliate leaves at various salinity levels by 55 days.

A. acutifolia (Plate 3b), A. goensis, (Plate 3e) and A. lanceolata were able to survive up to 6 dS/m salinity level without any severe salt injury symptoms. In A. acutifolia and A. goensis salt burning symptoms appeared on primary leaves, and then spread to trifoliate leaves at 4 and 6 dS/m. In A. lanceolata, stems were very

Plate 3d. Growth response of Atylosia sericea to different levels of salinity, 55 days after sowing.

Plate 3e. Growth response of Atylosia goensis to different levels of salinity, 55 days after sowing.

weak and plants developed a trailing habit at 4 and 6 dS/m. In A. lanceolata salt burning symptoms had spread to the trifoliate leaves at 6 dS/m., In A. acutifolia, A. goensis, and A. lanceolata, majority of the plants died at 8 and 10 dS/m in all the replications.

A. lineata, A. reticulata, and A. grandifolia were able to survive and grow up to 8 dS/m. At 4 and 6 dS/m, majority of the plants in the above species were able to grow without severe salt toxic symptoms. At 8 dS/m, these symptoms had spread to trifoliate leaves and wilting symptoms appeared in a few cases. None of these three species were able to survive at 10 dS/m.

A. albicans, A. cajanifolia, A. sericea (Plate 3d) and A. volubilis were the only species which could grow well up to 10 dS/m without any salt toxicity symptoms. However, in A. volubilis plants grown were stunted with salt burning symptoms at 10 dS/m. A comparison of salinity tolerance among wild species is presented in Table 4.5.1.

4.5.1 Effects on leaf area: In all the species, increasing salinity decreased the leaf area (Table 4.5.2 and Fig. 4.5.1). This reduction was least in A. albicans, and most in A. acutifolia. These 10 species of Atylosia were grouped into 3 categories depending on their level of tolerance to salinity: Category 1 - comprises species which could tolerate and grow at salinity levels up to 10 dS/m (A. albicans, A. sericea, A. cajanifolia and A. volubilis), Category 2 - comprises species which could tolerate and grow up to 8 dS/m (A. reticulata, A. grandifolia, and A. lineata), Category 3 - comprises species that could tolerate and grow up to

Table 4.5.1. Diagrammatic representation of salinity tolerance status (the ability to survive and grow) in pigeonpea and its wild relatives.

Tolerance up to 4 dS/m	Tolerance up to 6 dS/m	Tolerance upto 8 dS/m	Tolerance up to 10 dS/m	Tolerance up to 12 dS/m
				1. *A. albicans* 2. *A. platycarpa*
			1. *A. sericea* 2. *A. cajanifolia* 3. *A. volubilis*	
		1. ICPL 227 a. 2. *A. reticulata* 3. *A. grandifolia* 4. *A. lineata* 5. *A. scarabaeoides* 6. *D. ferruginea*		
	1. *A. goensis* 2. *A. lanceolata* 3. HY 3C b. 4. *A. acutifolia*			
R. albiflora				

a. Cultivated pigeonpea - tolerant genotype
b. Cultivated pigeonpea - sensitive genotype

Table 4.5.2. Effect of salinity on different species of Atylosia in relation to leaf area (cm2/pot).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1010	888 (88)	808 (80)	707 (70)	600 (59)
2.	A. sericea	340	272 (82)	231 (70)	204 (61)	153 (46)
3.	A. cajanifolia	714	515 (73)	394 (56)	321 (45)	221 (31)
4.	A. volubilis	1150	862 (76)	747 (66)	632 (55)	253 (22)
5.	A. reticulata	584	406 (70)	386 (67)	211 (37)	29 (5)
6.	A. grandifolia	634	390 (62)	251 (40)	134 (22)	11 (2)
7.	A. lineata	625	357 (57)	297 (47)	169 (27)	10 (2)
8.	A. goensis	1296	937 (73)	580 (42)	79 (7)	0 (0)
9.	A. lanceolata	408	192 (49)	145 (36)	56 (14)	12 (3)
10.	A. acutifolia	334	113 (34)	70 (21)	11 (4)	0 (0)

Leaf area : SE ± 24.2 LSD at 5% = 67.0 CV% = 12.3
% of control: SE ± 3.44 LSD at 5% = 9.53 CV% = 12.7
Note: Figures in parenthesis are ' % of control'

Table 4.5.3. Effect of salinity on different species of Atylosia in relation to shoot dry matter (g/pot).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	7.92	6.48 (82)	5.85 (74)	5.14 (65)	3.81 (48)
2.	A. sericea	9.31	7.54 (82)	6.24 (68)	5.49 (59)	4.00 (43)
3.	A. cajanifolia	8.70	6.38 (75)	5.10 (60)	4.09 (48)	2.87 (34)
4.	A. volubilis	10.13	7.20 (72)	6.28 (62)	5.37 (53)	2.53 (25)
5.	A. reticulata	4.83	3.27 (68)	3.19 (67)	1.73 (37)	0.43 (9)
6.	A. grandifolia	3.92	2.35 (59)	1.65 (43)	0.79 (21)	0.16 (4)
7.	A. lineata	7.14	3.93 (56)	2.97 (42)	1.86 (26)	0.71 (10)
8.	A. goensis	8.31	5.71 (69)	3.94 (48)	0.83 (10)	0.42 (5)
9.	A. lanceolata	5.72	2.76 (48)	2.21 (39)	1.12 (20)	0.29 (5)
10.	A. acutifolia	3.48	1.42 (41)	1.05 (30)	0.43 (12)	0.17 (5)

SE ± 0.215 LSD at 5% = 0.596 CV% = 10.9
SE ± 3.06 (for % of control) LSD at 5% = 8.48 CV% = 11.2
Note: Figures in parenthesis are '% of control'

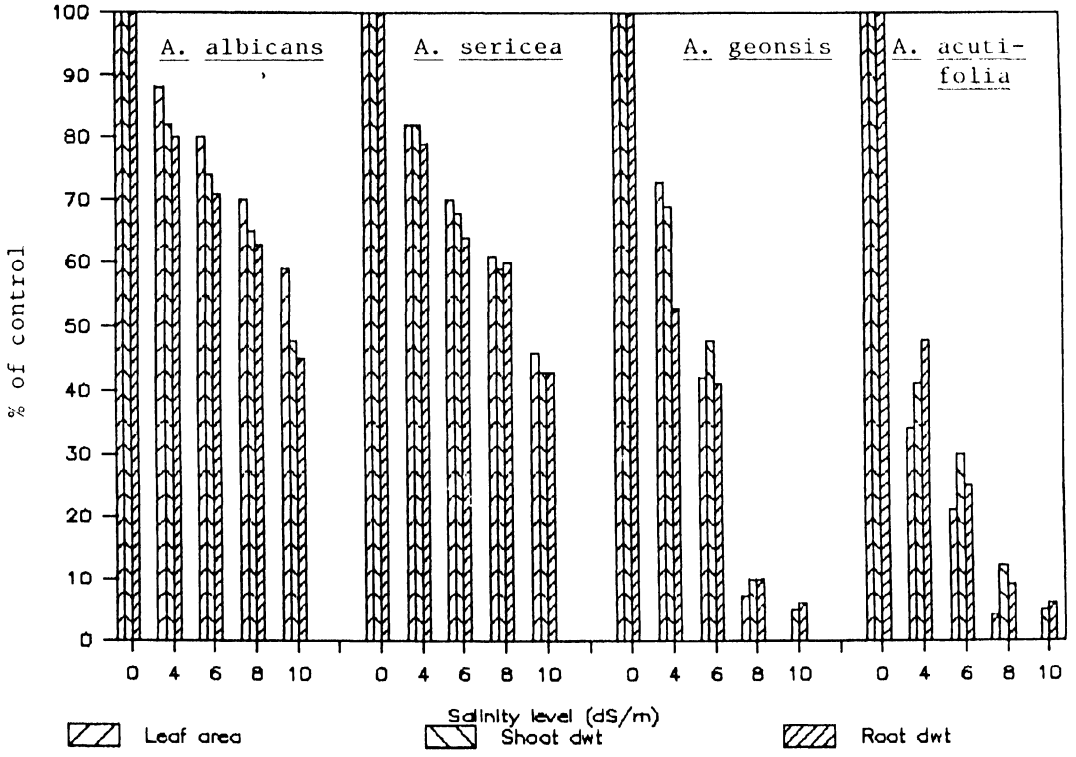

Fig. 4.5.1. Effect of salinity on plant growth of selected Atylosia species.

6 dS/m (A. goensis, A. lanceolata, A. acutifolia).

The range of variation in leaf area among species of Atylosia varied from 88% of control (A. albicans) to 34% of control (A.acutifolia) at 4 dS/m, from 80% (A. albicans) to 21% of the control (A. acutifolia) at 6 dS/m, from 70% (A. albicans) to 4% of the control (A. acutifolia) at 8 dS/m, and from 59% of control (A. albicans) to zero (A. acutifolia) at 10 dS/m.

4.5.2 Effects on shoot and root dry matter: In all the species, shoot and root dry matter decreased with increasing salinity (Table 4.5.3 and 4.5.4, Fig 4.5.1). The reduction in shoot and root dry matter was least in A. albicans and most in A. acutifolia and the trends were similar to the leaf area response. Root/shoot ratio of different species of Atylosia was not affected by increasing salinity in the medium (data not presented) but there were significant differences among species of Atylosia in the root/shoot ratio. The average root/shoot ratio was highest in A. reticulata (0.402) and lowest in A. volubilis (0.14).

4.5.3 Effects on free proline accumulation: In A. albicans, A. goensis, A. grandifolia and A. volubilis, there was no significant change in free proline levels with increasing salinity (Table 4.5.5). In A. acutifolia, there was two to three fold increase in leaf proline level at 6 dS/m and higher salinity levels. In A. reticulata, there was a slight increase at 6 dS/m and higher salinity levels. In A. cajanifolia, there was a large increase (120 times) of free proline in leaves at 10 dS/m. In A. lineata, there was a

Table 4.5.4. Effect of salinity on different species of Atylosia in relation to root dry matter (g/pot).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	2.30	1.84 (80)	1.63 (71)	1.45 (63)	1.04 (45)
2.	A. sericea	2.42	1.87 (79)	1.54 (64)	1.41 (60)	1.03 (43)
3.	A. cajanifolia	2.43	1.78 (74)	1.38 (57)	1.12 (47)	0.75 (32)
4.	A. volubilis	1.46	1.02 (70)	0.88 (61)	0.69 (47)	0.35 (24)
5.	A. reticulata	1.90	1.24 (67)	1.14 (62)	0.76 (41)	0.15 (8)
6.	A. grandifolia	1.32	0.77 (59)	0.51 (40)	0.25 (20)	0.05 (4)
7.	A. lineata	3.02	1.60 (53)	1.17 (39)	0.67 (23)	0.22 (7)
8.	A. goensis	1.51	0.79 (53)	0.61 (41)	0.15 (10)	0.09 (6)
9.	A. lanceolata	1.62	0.71 (45)	0.57 (36)	0.29 (19)	0.07 (4)
10.	A. acutifolia	1.38	0.65 (48)	0.34 (25)	0.12 (9)	0.08 (6)

SE ± 0.062 LSD at 5% = 0.173 CV% = 12.0

SE ± 3.14 (for % of control) LSD at 5% = 8.69 CV% = 11.9

Note: Figures in parenthesis are '% of control'

Table 4.5.5. Effect of salinity on different species of Atylosia in relation to leaf proline content (mg/g fresh wt).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.80	1.55	3.50	3.95	3.90
2.	A. sericea	0.80	1.65	28.95	56.90	52.00
3.	A. cajanifolia	0.60	1.35	3.30	3.95	60.70
4.	A. volubilis	1.45	0.75	0.95	0.85	3.70
5.	A. reticulata	1.95	1.50	1.35	1.45	8.10
6.	A. grandifolia	1.00	1.20	1.55	2.50	2.65
7.	A. lineata	0.45	10.40	10.70	10.30	47.00
8.	A. goensis	1.15	1.20	2.30	2.45	2.75
9.	A. lanceolata	1.40	1.60	21.85	21.45	26.00
10.	A. acutifolia	1.90	1.95	5.60	6.25	6.70

SE ± 0.98 LSD at 5% = 2.76 CV% = 16.8

significant increase of free proline from 4 dS/m to 10 dS/m. In A. lanceolata and A. sericea, this large increase was from 6 dS/m.

4.5.4 Ionic relations

4.5.4.1 Sodium: In A. albicans, there was no significant increase in the leaf sodium levels with increasing salinity (Table 4.5.6 and Fig 4.5.2). In A. sericea and A. cajanifolia, the increase in leaf sodium was significant only at 10 dS/m. In the other species, the increase was significant from 4 dS/m. The species in Category 1 (A. albicans, A. sericea, A. cajanifolia and A. volubilis) maintained significantly lower sodium in the leaf tissue at the higher salinity levels than the species of Category 2 (A. grandifolia, A. reticulata, A. lineata) and Cat.3 (A. goensis, A. lanceolata and A. acutifolia). The differences among species in leaf sodium increased with increasing salinity and became more clear at 8 and 10 dS/m. The species of Category3 which died at 8 dS/m had significantly higher leaf sodium than species of Category1 and Category2, which were able to tolerate and grow at such salinity levels. Similarly, the species belonging to Category 2 and 3 which died at 10 dS/m had significantly higher leaf sodium than the species of Category 1 which could tolerate and grow at this salinity level. The most tolerant species, A. albicans, maintained the lowest sodium (%) levels among species at each salinity level.

Stem sodium increased with increasing salinity except in A. albicans, where this increase was not significant (Table 4.5.7 and Fig 4.5.2). At 4 dS/m, stem sodium levels increased significantly in

Table 4.5.6. Effect of salinity on different species of Atylosia in relation to leaf sodium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.06	0.07	0.11	0.14	0.19
2.	A. sericea	0.04	0.11	0.18	0.18	0.23
3.	A. cajanifolia	0.06	0.15	0.16	0.18	0.23
4.	A. volubilis	0.04	0.20	0.23	0.27	0.30
5.	A. reticulata	0.05	0.16	0.20	0.42	1.04
6.	A. grandifolia	0.05	0.34	0.37	0.45	1.18
7.	A. lineata	0.06	0.34	0.57	1.29	1.55
8.	A. goensis	0.05	0.34	0.52	1.18	2.39
9.	A. lanceolata	0.05	0.50	0.55	0.69	1.35
10.	A. acutifolia	0.10	0.28	0.43	1.22	1.88

SE ± 0.063 LSD at 5% = 0.178 CV% = 19.5

Table 4.5.7. Effect of salinity on different species of Atylosia in relation to stem sodium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.07	0.09	0.11	0.13	0.15
2.	A. sericea	0.04	0.21	0.31	0.35	0.45
3.	A. cajanifolia	0.09	0.21	0.27	0.39	0.58
4.	A. volubilis	0.04	0.20	0.30	0.35	0.45
5.	A. reticulata	0.07	0.07	0.16	0.28	1.09
6.	A. grandifolia	0.07	0.30	0.38	0.59	1.89
7.	A. lineata	0.06	0.79	1.45	1.99	2.49
8.	A. goensis	0.06	0.41	0.49	1.47	3.05
9.	A. lanceolata	0.05	0.59	0.62	1.06	1.19
10.	A. acutifolia	0.07	0.31	0.70	2.32	3.97

SE ± 0.055 LSD at 5% = 0.156 CV% = 11.9

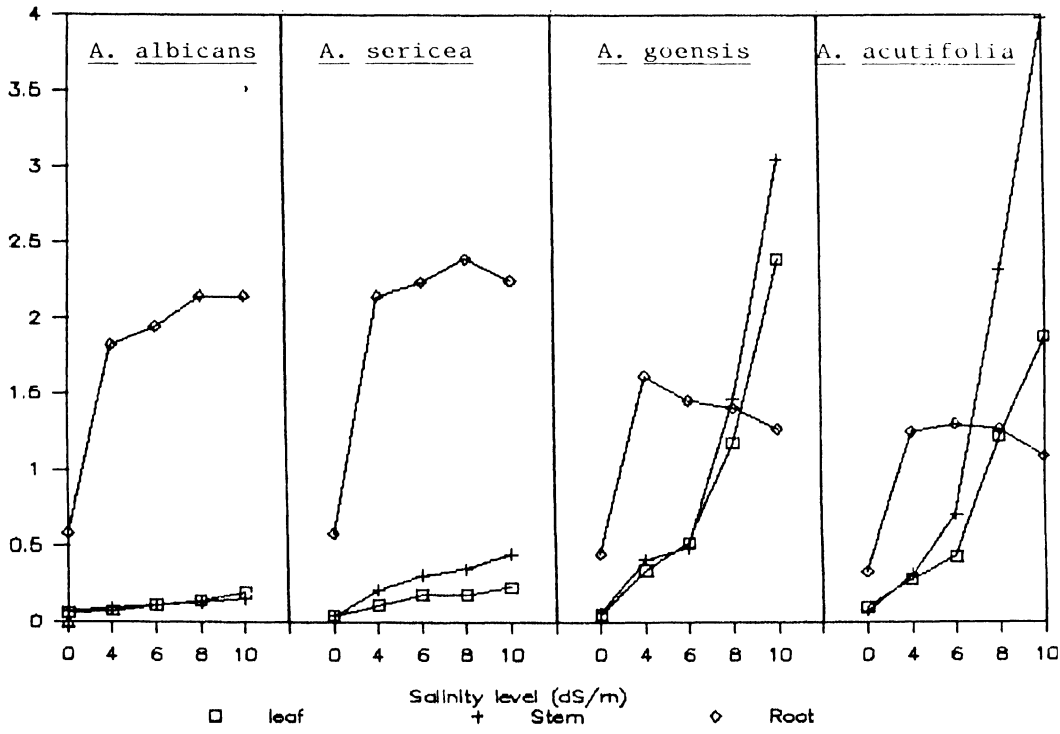

Fig. 4.5.2. Effect of salinity on tissue sodium concentration (%) of selected Atylosia species.

A. lineata, A. goensis and A. lanceolata. At 6 dS/m, stem sodium was increased significantly in A. lineata, A. lanceolata, A. acutifolia and A. goensis. At 8 dS/m, the stem sodium in species of Cat.2 (except A. reticulata) and Cat.3 were significantly higher than those of Cat.1. At 10 dS/m the species of Cat.1 maintained significantly lower sodium in the stem tissue than the species of Cat.2 and Cat.3.

Root sodium (%) levels were affected with increasing salinity (Table 4.5.8 and Fig 4.5.2). Root sodium (%) increased with increasing salinity in all the species. However, this increase was significant up to 10 dS/m only in A. albicans, and A. grandifolia. In the remaining species, there was a significant increase in the root sodium only up to 4 dS/m, but no further increase at higher salinity levels. In A. albicans, A. sericea, A. grandifolia and A. reticulata, the root sodium levels were significantly higher than those of the other species at various salinity levels.

4.5.4.2 Potassium: Leaf potassium was significantly affected with increasing salinity (Table 4.5.9 and Fig 4.5.3). In A. albicans, A. cajanifolia, A. sericea, A. volubilis, A. grandifolia, A. reticulata, leaf potassium increased with salinity and this increase in A. albicans and A. sericea (65% over control) was significantly higher than for A. cajanifolia, A. volubilis, A. reticulata and A. grandifolia. In A. lineata, leaf potassium increased only up to 6 dS/m and then declined at higher salinity levels. In A. lanceolata and A. goensis, the increase was up to 6 dS/m and at higher salinity levels it decreased. In A. acutifolia, there was no significant

Table 4.5.8. Effect of salinity on different species of Atylosia in relation to root sodium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.58	1.83	1.95	2.15	2.15
2.	A. sericea	0.58	2.15	2.24	2.39	2.25
3.	A. cajanifolia	0.43	1.81	1.90	2.01	1.82
4.	A. volubilis	0.50	1.60	1.64	1.68	1.57
5.	A. reticulata	0.35	2.08	2.19	2.29	2.31
6.	A. grandifolia	0.51	2.27	2.35	2.72	2.74
7.	A. lineata	0.45	1.77	1.80	1.50	1.50
8.	A. goensis	0.45	1.62	1.46	1.41	1.27
9.	A. lanceolata	0.58	1.93	1.79	1.17	1.11
10.	A. acutifolia	0.33	1.25	1.30	1.27	1.09

SE ± 0.16 LSD at 5% = 0.442 CV% = 14.1

Table 4.5.9. Effect of salinity on different species of Atylosia in relation to leaf potassium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.15	1.49 (130)	1.78 (155)	1.80 (157)	1.90 (165)
2.	A. sericea	1.41	1.79 (127)	2.19 (155)	2.23 (158)	2.32 (165)
3.	A. cajanifolia	1.38	1.49 (108)	1.60 (116)	1.69 (122)	1.71 (124)
4.	A. volubilis	1.08	1.19 (110)	1.41 (130)	1.37 (129)	1.37 (129)
5.	A. reticulata	1.60	1.71 (106)	1.75 (109)	1.95 (121)	1.72 (107)
6.	A. grandifolia	1.55	1.69 (109)	1.74 (113)	1.77 (114)	1.80 (116)
7.	A. lineata	1.32	1.94 (150)	2.11 (160)	1.80 (136)	1.18 (90)
8.	A. goensis	1.21	1.66 (137)	1.73 (143)	1.05 (87)	0.95 (76)
9.	A. lanceolata	1.71	1.83 (107)	1.84 (108)	1.35 (79)	1.30 (76)
10.	A. acutifolia	1.48	1.41 (95)	1.38 (93)	0.80 (54)	0.70 (47)

SE ± 0.095 LSD at 5% = 0.269 CV% = 8.6

Note. Figures in parenthesis are '% of control'

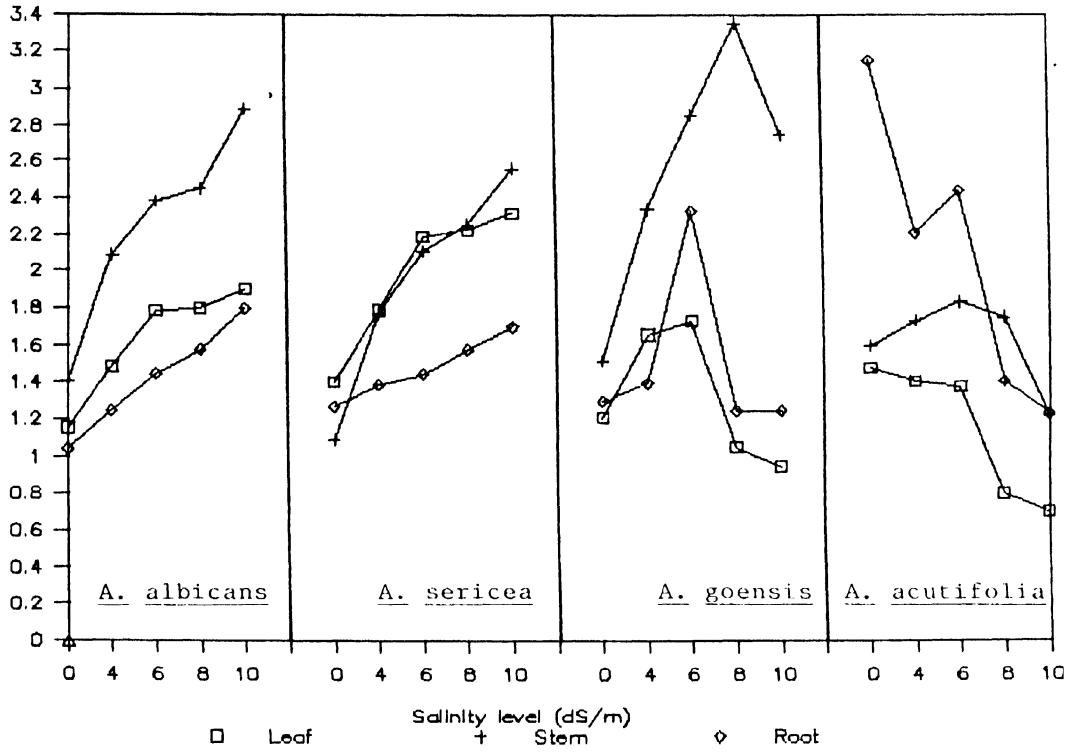

Fig. 4.5.3. Effect of salinity on tissue potassium concentration (%) of selected Atyloisa species.

change in leaf potassium up to 6 dS/m, but it significantly decreased to about 50% of its control at 8 and 10 dS/m, where the plants failed to survive.

Stem potassium (%) was significantly affected with increasing salinity (Table 4.5.10 and Fig 4.5.3). In all the species, stem potassium increased with increasing salinity. However, this increase was significantly higher in A. albicans and A. sericea (about 100% increase over their respective controls) than the other species. In A. acutifolia, where there was no significant change in the stem potassium up to 8 dS/m had decreased at 10 dS/m.

Root potassium (%) increased with salinity (Table 4.5.11 and Fig 4.5.3). In the species: A. albicans, A. cajanifolia, A. sericea, and A. lineata there was a significant increase in the root potassium (about 73% over their respective controls) with increasing salinity. In A. goensis and A. lanceolata, this increase was only up to 6 dS/m and there was a decline at higher salinity levels. In A. volubilis and A. grandifolia, there was no significant change in the root potassium with increasing salinity. In A. reticulata and A. acutifolia, root potassium levels decreased with increasing salinity.

4.5.4.3 Potassium/sodium (K/Na) ratio: The K/Na ratio in leaf and stem decreased with increasing salinity (Tables 4.5.12 and 4.5.13). In A. albicans, A. cajanifolia, and A. sericea, leaf and stem K/Na ratio was less affected than in the other species. However these differences were not statistically significant. Root KNa ratio also decreased significantly with increasing salinity in all the species. (Table 4.5.14).

Table 4.5.10. Effect of salinity on different species of Atylosia in relation to stem potassium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.41	2.09 (148)	2.38 (169)	2.45 (174)	2.89 (206)
2.	A. sericea	1.09	1.77 (162)	2.11 (194)	2.26 (207)	2.56 (235)
3.	A. cajanifolia	1.44	2.04 (142)	2.29 (159)	2.30 (159)	2.35 (163)
4.	A. volubilis	1.30	1.62 (125)	1.81 (139)	1.92 (148)	2.21 (170)
5.	A. reticulata	1.96	2.17 (111)	2.29 (117)	2.62 (134)	2.23 (114)
6.	A. grandifolia	2.06	2.18 (106)	2.38 (116)	2.60 (126)	3.14 (152)
7.	A. lineata	1.28	2.23 (174)	2.33 (182)	1.80 (141)	1.45 (113)
8.	A. goensis	1.52	2.34 (154)	2.83 (186)	3.35 (220)	2.75 (185)
9.	A. lanceolata	1.65	2.44 (148)	2.71 (164)	2.30 (139)	2.04 (124)
10.	A. acutifolia	1.60	1.73 (108)	1.83 (114)	1.75 (109)	1.22 (76)

SE ± 0.119 LSD at 5% = 0.339 CV% = 8.0

Note. Figures in parenthesis are '% of control'

Table 4.5.11. Effect of salinity on different species of Atylosia in relation to root potassium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.04	1.25 (120)	1.45 (139)	1.58 (152)	1.80 (173)
2.	A. sericea	1.27	1.39 (109)	1.45 (114)	1.58 (124)	1.70 (134)
3.	A. cajanifolia	1.55	2.00 (129)	2.23 (144)	2.38 (154)	2.70 (174)
4.	A. volubilis	1.51	1.54 (102)	1.55 (103)	1.55 (103)	1.65 (109)
5.	A. reticulata	2.38	1.99 (84)	1.92 (81)	1.66 (70)	1.25 (52)
6.	A. grandifolia	2.37	2.40 (101)	2.23 (94)	2.15 (91)	2.05 (86)
7.	A. lineata	1.67	2.27 (136)	3.08 (184)	2.70 (162)	2.35 (141)
8.	A. goensis	1.30	1.40 (108)	2.33 (179)	1.25 (96)	1.25 (96)
9.	A. lanceolata	1.85	1.93 (104)	2.40 (130)	1.44 (78)	0.99 (54)
10.	A. acutifolia	3.15	2.21 (70)	2.44 (77)	1.41 (45)	1.23 (39)

SE ± 0.125 LSD at 5% = 0.356 CV% = 9.6

Note: Figures in parenthesis are '% of control'

Table 4.5.14. Effect of salinity on different species of Atylosia in relation to root potassium/sodium ratio.

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.79	0.68 (38)	0.74 (41)	0.73 (40)	0.85 (47)
2.	A. sericea	2.19	0.65 (30)	0.66 (30)	0.66 (30)	0.76 (35)
3.	A. cajanifolia	3.64	1.11 (30)	1.17 (32)	1.13 (31)	1.49 (41)
4.	A. volubilis	3.06	0.99 (32)	0.98 (32)	0.94 (31)	1.05 (34)
5.	A. reticulata	7.11	0.96 (14)	0.87 (12)	0.72 (10)	0.54 (8)
6.	A. grandifolia	4.64	1.09 (23)	0.95 (20)	0.79 (17)	0.75 (16)
7.	A. lineata	3.92	1.28 (33)	1.74 (44)	1.85 (47)	1.59 (41)
8.	A. goensis	3.83	0.86 (22)	1.64 (43)	0.92 (24)	1.09 (28)
9.	A. lanceolata	3.24	1.00 (31)	1.34 (41)	1.24 (38)	0.92 (28)
10.	A. acutifolia	9.57	1.78 (19)	1.87 (20)	1.11 (12)	1.14 (12)

SE ± 0.376 LSD at 5% = 1.07 CV% = 31.0

Note: Figures in parenthesis are '% of control'

Table 4.5.15. Effect of salinity on different species of Atylosia in relation to leaf calcium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	2.95	3.05	3.15	3.80	4.20
2.	A. sericea	1.09	1.47	1.61	1.75	1.85
3.	A. cajanifolia	1.25	1.30	1.50	1.60	1.60
4.	A. volubilis	1.07	1.23	1.31	1.68	1.71
5.	A. reticulata	1.16	1.35	1.40	1.60	2.50
6.	A. grandifolia	1.10	1.20	1.80	1.80	2.85
7.	A. lineata	0.96	1.11	1.58	2.46	2.95
8.	A. goensis	1.25	1.79	1.82	2.20	3.04
9.	A. lanceolata	1.27	1.71	2.36	2.53	2.90
10.	A. acutifolia	1.03	1.46	1.55	1.71	2.14

SE ± 0.168 LSD at 5% = 0.476 CV% = 12.7

4.5.4.4 Calcium: In all the Atylosia species tested, leaf Calcium levels increased with salinity (Table 4.5.15). The interaction between species and salinity treatment was significant. The leaf Ca in A. albicans was significantly higher at all salinity levels, including control. Stem and root Ca (%) of different Atylosia species increased with increasing salinity (Tables 4.5.16 and 4.5.17). Also, the interaction between species and salinity treatment in the stem and root Ca was significant.

4.5.4.5 Magnesium: In A. albicans, A. sericea and A. cajanifolia, and A. acutifolia there was no significant change in the leaf Mg (%) with increasing salinity (Table 4.5.18). But in other species it decreased (about 50 to 75% reduction) with increasing salinity in the medium. In A. albicans, A. cajanifolia, A. sericea, A. reticulata, and A. lanceolata there was no significant change in the stem Mg (%) with increasing salinity (Table 4.5.19). In A. grandifolia, A. goensis and A. acutifolia, stem Mg increased with increasing salinity in the medium. In A. lineata, stem Mg decreased with increasing salinity.

In A. albicans, A. acutifolia, A. cajanifolia, A. goensis, A. lanceolata, A. reticulata and A. volubilis, root Mg decreased with increasing salinity. This decrease was very severe (90% reduction at 10 dS/m) in A. lanceolata (Table 4.5.20). In A. lineata and A. sericea, root Mg was not significantly affected by salinity.

4.5.4.6 Chloride: In all the species, leaf Cl (%) increased with the increasing salinity (Table 4.5.21 and Fig 4.5.4). However, this

Table 4.5.16. Effect of salinity on different species of Atylosia in relation to stem calcium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.75	2.15	2.30	2.50	2.70
2.	A. sericea	1.02	1.73	1.74	1.83	1.95
3.	A. cajanifolia	1.16	1.95	1.96	1.98	2.05
4.	A. volubilis	0.69	0.99	1.08	1.14	1.30
5.	A. reticulata	1.29	1.55	1.91	1.96	2.65
6.	A. grandifolia	1.31	1.60	1.95	2.15	3.87
7.	A. lineata	1.85	2.30	2.40	2.49	3.26
8.	A. goensis	0.73	1.17	1.24	1.55	3.20
9.	A. lanceolata	1.45	2.06	2.18	2.32	2.70
10.	A. acutifolia	1.15	1.64	2.26	2.74	3.07

SE ± 0.149 LSD at 5% = 0.422 CV% = 11.0

Table 4.5.17. Effect of salinity on different species of Atylosia in relation to root calcium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.80	0.95	1.10	1.25	1.30
2.	A. sericea	0.56	0.60	0.85	0.93	1.10
3.	A. cajanifolia	0.57	0.61	0.67	0.75	0.76
4.	A. volubilis	0.55	0.75	0.85	0.85	0.85
5.	A. reticulata	0.54	0.60	0.73	0.80	0.85
6.	A. grandifolia	0.81	0.98	1.10	1.15	1.20
7.	A. lineata	0.54	0.59	0.73	0.73	0.74
8.	A. goensis	0.33	0.45	0.71	1.00	1.25
9.	A. lanceolata	0.46	0.58	0.65	0.75	0.90
10.	A. acutifolia	0.52	0.69	0.70	1.17	1.20

SE ± 0.085 LSD at 5% = 0.241 CV% = 15.0

Table 4.5.18. Effect of salinity on different species of Atylosia in relation to leaf magnesium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.16	0.16	0.15	0.16	0.17
2.	A. sericea	0.22	0.22	0.21	0.21	0.21
3.	A. cajanifolia	0.19	0.19	0.18	0.19	0.18
4.	A. volubilis	0.29	0.19	0.18	0.17	0.17
5.	A. reticulata	0.35	0.25	0.20	0.20	0.18
6.	A. grandifolia	0.45	0.33	0.31	0.20	0.20
7.	A. lineata	0.33	0.27	0.21	0.21	0.20
8.	A. goensis	0.58	0.46	0.44	0.25	0.18
9.	A. lanceolata	0.45	0.40	0.39	0.25	0.15
10.	A. acutifolia	0.30	0.30	0.31	0.32	0.31

SE ± 0.029 LSD at 5% = 0.0827 CV% = 16.2

Table 4.5.19. Effect of salinity on different species of Atylosia in relation to stem magnesium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.10	0.15	0.15	0.15	0.18
2.	A. sericea	0.14	0.17	0.16	0.14	0.14
3.	A. cajanifolia	0.19	0.20	0.28	0.29	0.29
4.	A. volubilis	0.13	0.11	0.11	0.11	0.11
5.	A. reticulata	0.15	0.12	0.11	0.10	0.10
6.	A. grandifolia	0.39	0.41	0.41	0.55	0.93
7.	A. lineata	0.50	0.39	0.35	0.28	0.28
8.	A. goensis	0.39	0.40	0.39	0.56	0.70
9.	A. lanceolata	0.45	0.49	0.51	0.51	0.55
10.	A. acutifolia	0.29	0.32	0.35	0.80	0.80

SE ± 0.03 LSD at 5% = 0.074 CV% = 11.6

Table 4.5.20. Effect of salinity on different species of Atylosia in relation to root magnesium concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	1.08	0.69	0.65	0.69	0.69
2.	A. sericea	0.51	0.45	0.38	0.35	0.35
3.	A. caianifolia	1.10	0.75	0.70	0.70	0.70
4.	A. volubilis	1.21	0.41	0.35	0.33	0.28
5.	A. reticulata	1.30	0.55	0.45	0.40	0.40
6.	A. grandifolia	0.98	0.65	0.45	0.44	0.44
7.	A. lineata	1.10	1.15	1.15	1.15	1.15
8.	A. goensis	1.10	0.30	0.35	0.30	0.30
9.	A. lanceolata	1.08	0.53	0.33	0.15	0.15
10.	A. acutifolia	0.89	0.59	0.49	0.34	0.27

SE ± 0.053 LSD at 5% = 0.144 CV% = 12.0

Table 4.5.21. Effect of salinity on different species of Atylosia in relation to leaf chloride concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.15	1.30	1.50	1.65	2.20
2.	A. sericea	0.10	0.83	0.97	1.36	1.94
3.	A. caianifolia	0.11	0.35	0.53	0.78	1.16
4.	A. volubilis	0.15	1.06	1.59	1.84	2.32
5.	A. reticulata	0.12	0.53	0.83	1.56	2.87
6.	A. grandifolia	0.08	0.34	0.68	1.33	2.53
7.	A. lineata	0.13	2.80	3.61	4.55	5.61
8.	A. goensis	0.15	0.19	1.87	2.42	5.73
9.	A. lanceolata	0.13	1.23	2.10	3.30	3.60
10.	A. acutifolia	0.09	0.28	1.01	2.43	4.54

SE ± 0.143 LSD at 5% = 0.407 CV% = 12.7

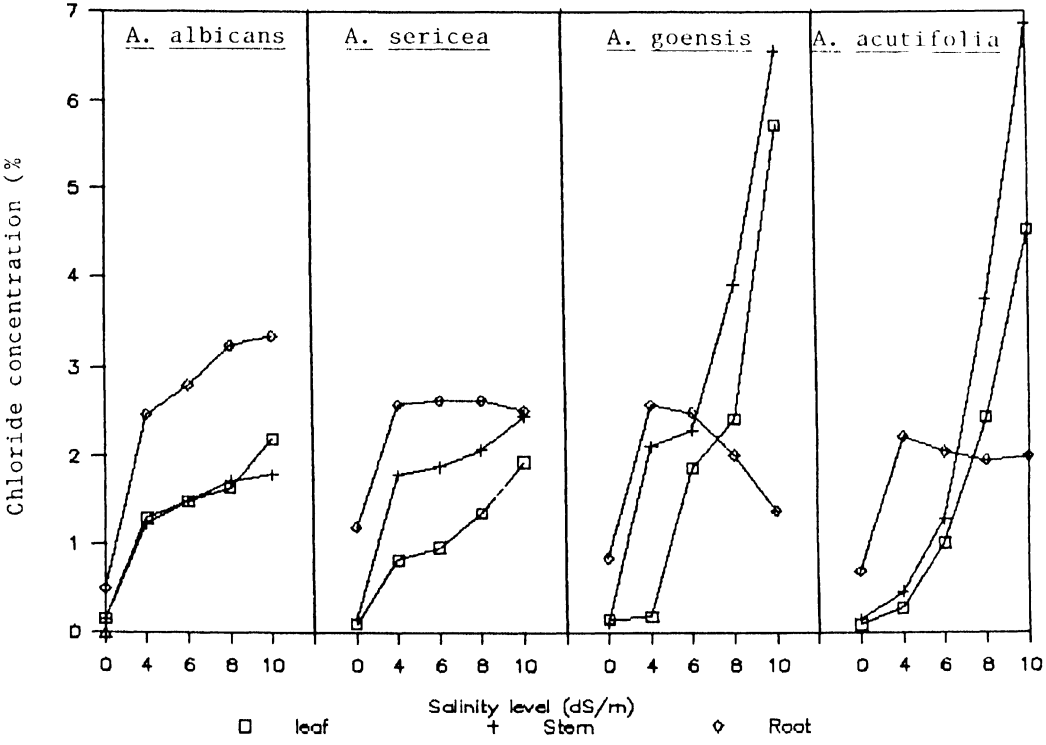

Fig. 4.5.4. Effect of salinity on tissue chloride concentration (%) of selected Atylosia species.

increase was significantly highest in A. lineata, and lowest in A. cajanifolia. In A. lineata, A. goensis, A. lanceolata and A. acutifolia at 8 and 10 dS/m, leaf chloride was significantly higher than in the species A. albicans, A. cajanifolia, A. sericea, A. reticulata and A. grandifolia.

Stem Cl levels (%) increased with increasing salinity (Table 4.5.22 and Fig 4.5.4). There were significant differences among species of Atylosia in the stem Cl levels. In A. volubilis, the average Cl level in the stem tissue was lowest (1.10%), and it was highest in A. lineata (3.40%).

In A. albicans, A. cajanifolia, A. sericea, A. volubilis, A. grandifolia, root Cl level increased with salinity (Table 4.5.23 and Fig 4.5.4). In A. lineata and A. lanceolata, this increase was only up to 4 dS/m and in A. reticulata, it was up to 6 dS/m; root Cl in these species then declined at 8 and 10 dS/m. In A. acutifolia, there was an increase in the root Cl only at 4 dS/m.

4.5.4.7 Manganese: In A. albicans, A. goensis, A. lineata, A. sericea and A. volubilis, leaf Mn levels increased with salinity (Table 4.5.24). In A. grandifolia, A. lanceolata, salinity decreased the leaf Mn levels. In A. acutifolia, A. cajanifolia, A. reticulata, there was no significant change in the leaf Mn levels with increasing salinity.

4.5.4.8 Zinc: The Zn content in leaves increased with increasing salinity in all the species (Table 4.5.24).

Table 4.5.22. Effect of salinity on different species of Atylosia in relation to stem chloride concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.15	1.23	1.50	1.73	1.80
2.	A. sericea	0.15	1.80	1.89	2.08	2.45
3.	A. caianifolia	0.18	1.26	1.77	1.99	2.10
4.	A. volubilis	0.15	0.75	1.38	1.46	1.77
5.	A. reticulata	0.11	1.17	1.37	1.93	3.44
6.	A. grandifolia	0.08	0.64	0.80	1.62	2.43
7.	A. lineata	0.23	3.11	3.72	4.29	5.65
8.	A. goensis	0.11	2.12	2.30	3.90	6.57
9.	A. lanceolata	0.13	1.20	1.63	2.58	2.99
10.	A. acutifolia	0.15	0.46	1.29	3.75	6.86

SE ± 0.167 LSD at 5% = 0.475 CV% = 12.6

Table 4.5.23. Effect of salinity on different species of Atylosia in relation to root chloride concentration (%).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
1.	A. albicans	0.50	2.46	2.80	3.25	3.35
2.	A. sericea	1.20	2.58	2.63	2.63	2.51
3.	A. caianifolia	0.75	2.68	2.70	2.86	2.84
4.	A. volubilis	1.15	2.19	2.37	2.39	2.60
5.	A. reticulata	1.15	3.44	3.17	2.64	2.12
6.	A. grandifolia	1.22	2.76	2.59	2.67	4.36
7.	A. lineata	1.05	4.31	4.98	4.11	2.07
8.	A. goensis	0.85	2.58	2.49	2.02	1.39
9.	A. lanceolata	1.30	3.64	3.48	2.40	1.60
10.	A. acutifolia	0.70	2.22	2.05	1.95	2.00

SE ± 0.16 LSD at 5% = 0.46 CV% = 9.5

Table 4.5.24. Effect of salinity on different species of Atylosia in relation to leaf manganese, zinc and iron concentration (ppm).

Sl.No.	Atylosia sp.	Salinity treatment (dS/m) 0	4	6	8	10
		Leaf manganese concentration (ppm)				
1.	A. albicans	71	90	131	144	150
2.	A. sericea	114	120	146	162	174
3.	A. cajanifolia	185	195	200	205	205
4.	A. volubilis	95	115	117	125	147
5.	A. reticulata	123	135	145	153	155
6.	A. grandifolia	448	251	190	180	180
7.	A. lineata	95	120	149	163	219
8.	A. goensis	310	486	666	678	695
9.	A. lanceolata	825	390	375	360	338
10.	A. acutifolia	214	206	188	185	175
SE ± 16.3		LSD at 5% = 46.2		CV% = 9.8		
		Leaf zinc concentration (ppm).				
1.	A. albicans	23	24	28	29	29
2.	A. sericea	39	41	41	44	47
3.	A. cajanifolia	45	45	46	42	42
4.	A. volubilis	21	23	27	29	33
5.	A. reticulata	27	30	35	37	60
6.	A. grandifolia	32	35	40	44	48
7.	A. lineata	33	36	38	48	53
8.	A. goensis	48	51	52	58	64
9.	A. lanceolata	39	45	51	50	51
10.	A. acutifolia	26	30	34	57	63
SE ± 1.651		LSD at 5% = 4.67		CV% = 5.8		
		Leaf iron concentration (ppm).				
1.	A. albicans	105	125	135	143	167
2.	A. sericea	160	177	210	215	255
3.	A. cajanifolia	188	234	276	285	290
4.	A. volubilis	95	90	75	65	55
5.	A. reticulata	210	140	133	120	115
6.	A. grandifolia	118	125	130	135	141
7.	A. lineata	112	118	118	115	140
8.	A. goensis	392	395	430	450	480
9.	A. lanceolata	125	151	200	217	246
0.	A. acutifolia	172	178	285	350	450
SE ± 13.9		LSD at 5% = 39.4				

4.5.4.9 Iron: In A. albicans, A. acutifolia, A. cajanifolia, A. goensis, A. lanceolata, and A. sericea leaf Fe levels increased with salinity (Table 4.5.24). In A. reticulata, and A. volubilis leaf Fe levels were significantly decreased with salinity. In A. grandifolia, and A. lineata, there was no significant change in the leaf Fe level with salinity.

4.6A Response of pigeonpea-Rhizobium symbiosis to salinity

The objective of this investigation was to study the response of the pigeonpea-Rhizobium symbiosis to salinity and to assess rhizobial variation in symbiotic ability under salinity stress. Pigeonpea genotype ICPL 227 was used in this study. Five rhizobial strains, IC 3024, IC 3506, IC 3484, IC 3087 and IC 3195, were selected on the basis of their growth habit, tolerance to salinity in YMA medium, ecological origin, and symbiotic ability under normal conditions. These details are presented in Table 3.4 (Materials and Methods). There were 4 salinity treatments - 0, 4, 6, 8 dS/m and 6 nitrogen treatments - fed with inorganic nitrogen (N-fed) or inoculated with either IC 3024, IC 3506, IC 3484, IC 3087 and IC 3195. The experiment was done with randomized complete block design, replicated four times. Salinity treatments were imposed 14 days after sowing and rhizobial inoculation was done immediately after that. The N-fed treatment was given 50 ppm nitrogen as ammonium nitrate at 28 days after sowing, i.e two weeks after rhizobial inoculation, when the symbiotic system usually becomes functional. Plants were harvested 65 days after sowing.

4.6B Functioning of the pigeonpea-Rhizobium symbiosis in relation to time of inoculation

The purpose of this experiment was to study whether the early stages of establishment of the symbiosis are more sensitive to salinity compared to the functioning of the symbiotic system. Pigeonpea genotype ICPL 227 and rhizobial strains IC 3024 and IC 3195

were selected for this study. There were four salinity treatments, 0, 4, 6 and 8 dS/m and four rhizobial treatments: IC 3024 early (i.e inoculated at the time of sowing), IC 3024 late (i.e inoculated after the salinity treatments were imposed), IC 3195 early and IC 3195 late. Salinity treatments were imposed 14 days after sowing. The experiment was done in randomized complete block design, replicated four times. Plants were harvested 65 days after sowing.

Findings (4.6A and 4.6B)

Plants were healthy and green by 15 days after rhizobial inoculation in both early and late inoculated treatments, indicating the functioning of the symbiotic nitrogen fixing system. Salt burning symptoms appeared on the primary leaves at 6 and 8 dS/m salinity levels but they were not severe in any of the treatments. Plant growth in the N-fed treatment was slightly better than the rhizobial inoculated treatments but these differences were more prominent at 8 dS/m. Similarly, the differences among the rhizobial strains increased with salinity. Among the rhizobial treatments, plants inoculated with IC 3506 and IC 3087 appeared better than those inoculated with IC 3024, IC 3484, and IC 3195, at various salinity levels.

For IC 3024, the early-inoculated plants appeared better than late inoculated ones at the various salinity levels. But in the control (without salinity stress), there were no visual differences between early and late inoculation. In early inoculated IC 3195, plants did not nodulate at any of the salinity levels including control, for unknown reasons. This led to severe nitrogen deficiency

in all the plants of this treatment and this treatment was therefore dropped from the analysis of the results.

4.6.1 Effect on leaf area: In all the nitrogen treatments, leaf area decreased with increasing salinity (Table 4.6.1). However, this decrease was more in the rhizobial-inoculated compared to the N-fed treatment. At 4 dS/m, leaf area in the IC 3024 and IC 3484 rhizobial treatments, was significantly more affected than in the rhizobial treatments IC 3506, IC 3087 and IC 3195, where the leaf area response was similar to the N-fed treatment and the differences were not significant. At 6 dS/m, the rhizobial treatments IC 3024 and IC 3484 were significantly more affected than IC 3506, IC 3087 and IC 3195 and the differences among IC 3506, IC 3087, and IC 3195 treatments were not significant. At 8 dS/m, the rhizobial treatments, IC 3506 and IC 3087 were significantly less affected than IC 3024, IC 3506 and IC 3195.

In both early and late inoculation treatments of IC 3024, leaf area was significantly affected with increasing salinity in the medium (Table 4.6.2). However, the relative reduction was greater in the late inoculation treatment compared to the early inoculation. At 4 dS/m, there was no difference between the early and late inoculation treatments whereas at 6 and 8 dS/m, the leaf area in the early inoculated treatment was significantly less affected compared to the late inoculated treatment.

4.6.2 Effect on shoot dry matter: Shoot dry matter in all the nitrogen treatments significantly decreased with increasing salinity

Table 4.6.1. Effect of salinity on leaf area, shoot and root dry matter of pigeonpea genotype ICPL 227 inoculated with different rhizobial strains.

Rhizobial strains	Salinity level (dS/m) 0	4	6	8
		Leaf area (cm2/pot)		
IC 3087	629	422 (67)	316 (50)	224 (36)
IC 3506	614	399 (66)	305 (50)	230 (38)
IC 3195	559	377 (68)	270 (49)	70 (13)
IC 3484	586	326 (56)	211 (34)	71 (12)
IC 3024	656	371 (56)	178 (27)	59 (9)
Nitrogen fed	791	567 (72)	467 (59)	373 (47)
SE ± 17.6		LSD at 5% = 48.8		CV% = 9.0
SE ± 2.72 (for % of control)		LSD at 5%= 7.7		CV% = 9.2
		Shoot dry matter (g/pot)		
IC 3087	4.84	3.49 (72)	2.68 (55)	2.01 (41)
IC 3506	4.65	3.32 (72)	2.49 (54)	1.92 (41)
IC 3195	4.32	3.24 (75)	2.24 (52)	0.66 (15)
IC 3484	4.31	2.86 (66)	1.80 (42)	0.71 (17)
IC 3024	4.84	3.21 (67)	1.48 (31)	0.68 (14)
Nitrogen fed	6.00	4.62 (77)	3.46 (58)	3.11 (52)
SE ± 0.143		LSD at 5% = 0.404		CV% = 9.0
SE ± 2.38 (for % of control)		LSD at 5%= 6.71		CV% = 7.5
		Root dry matter (g/pot)		
IC 3087	1.22	1.06 (87)	0.77 (63)	0.55 (46)
IC 3506	1.32	1.05 (80)	0.77 (58)	0.58 (44)
IC 3195	1.25	0.99 (79)	0.78 (63)	0.19 (15)
IC 3484	1.23	0.90 (73)	0.56 (45)	0.23 (18)
IC 3024	1.46	1.16 (80)	0.56 (38)	0.25 (17)
Nitrogen fed	1.55	1.29 (84)	1.01 (66)	0.84 (54)
SE ± 0.044		LSD at 5% = 0.123		CV% = 9.4
SE ± 3.2 (for % of control)		LSD at 5%= 9.1		CV% = 9.5

Note: figures in parenthesis are '% of control'

Table 4.6.2. Effect of time of inoculation with IC 3024 on leaf area, shoot and root dry matter of pigeonpea genotype ICPL 227 at different salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8
		Leaf area (cm2/pot)		
Early	769	461 (60)	413 (54)	309 (40)
Late	656	371 (56)	178 (27)	59 (9)
SE ± 17.6		LSD at 5% = 48.8		CV% = 9.0
SE ± 2.72 (for % of control)		LSD at 5%= 7.7		CV% = 9.2
		Shoot dry matter (g/pot)		
Early	6.09	4.21 (70)	3.14 (53)	2.55 (42)
Late	4.84	3.21 (66)	1.48 (31)	0.68 (14)
SE ± 0.143		LSD at 5% = 0.404		CV% = 9.0
SE ± 2.38 (for % of control)		LSD at 5%= 7.5		CV% = 7.5
		Root dry matter (g/pot)		
Early	1.51	1.24 (82)	0.87 (58)	0.68 (45)
Late	1.46	1.16 (80)	0.56 (38)	0.25 (17)
SE ± 0.044		LSD at 5% = 0.123		CV% = 9.4
SE ± 3.20 (for % of control)		LSD at 5% = 9.0		CV% = 9.5

Note: Figures in parenthesis are '% of control'

(Table 4.6.1). At 4 and 6 dS/m, the rhizobial treatments IC 3024 and IC 3484 were more affected than the IC 3506, IC 3087, IC 3195 and N-fed treatments. The differences among IC 3506, IC 3087, IC 3195 and the N-fed treatment in the shoot dry matter response were not significant. At 8 dS/m, the shoot dry matter in the N-fed treatment was significantly less affected than the rhizobial treatments. Among rhizobial treatments, IC 3506 and IC 3087 were significantly less affected than the IC 3024, IC 3484 and IC 3195.

Shoot dry matter significantly decreased with increasing salinity in both early and late inoculated treatments of IC 3024 (Table 4.6.2). At 4 dS/m salinity level, the shoot dry matter response in the early and late inoculated IC 3024 treatments was similar and there were no significant differences between them. But at 6 and 8 dS/m salinity levels, the early inoculated IC 3024 rhizobial treatment was significantly less affected than the late inoculated treatment.

4.6.3 Efects on root dry matter: Root dry matter was significantly affected by increasing salinity in all the treatments (Table 4.6.1). At 4 dS/m, root dry matter in the rhizobial treatments IC 3506, IC 3087, IC 3195 and the N-fed treatment, was significantly less affected than in IC 3024 and IC 3484. At 6 dS/m, the N-fed treatment was less affected than the rhizobial treatments. Among rhizobial treatments, IC 3506, IC 3087 and IC 3195 were significantly less affected than IC 3024 and IC 3484. At 8 dS/m, the N-fed treatment was significantly less affected than the rhizobial inoculated treatments. Among rhizobial treatments, IC 3506 and IC 3087 were significantly less affected than IC 3024, IC 3484 and IC 3195.

Root dry matter significantly decreased with increasing salinity in both early and late inoculated treatments (Table 4.6.2). However, at 6 and 8 dS/m salinity levels, root dry matter in the early inoculated treatment was significantly less affected than that in the late inoculated treatment.

4.6.4 Effects of salinity on the nodulation and nitrogenase activity

4.6.4.1 Effects on nodule number: In plants inoculated with IC 3087, the nodule number was highest (498), whereas, it was lowest (80) in IC 3024. In IC 3087, nodule number was significantly increased at 4 and 6 dS/m and remained unaffected at 8 dS/m (Table 4.6.3 and Plate 4). In the remaining rhizobial strains (IC 3024, IC 3506, IC 3484 and IC 3195), nodule number decreased with increasing salinity. In IC 3506, this reduction was significantly less than in IC 3024, IC 3484, IC 3195.

Nodule number decreased significantly with salinity in both early and late inoculated IC 3024 treatments (Table 4.6.4). However, this reduction was significantly less in the early inoculated treatment and the differences between them increased with salinity. At 8 dS/m, in the late inoculated treatment there was a severe reduction in the number of nodules (97% decrease), as 55% reduction in the early inoculated treatment.

4.6.4.2 Effect on nodule dry matter: Total nodule dry matter significantly decreased with increasing salinity in all the rhizobial strains (Table 4.6.3). In IC 3087 and IC 3506, total nodule dry

Table 4.6.3. Effect of salinity on nodule number, and nodule dry weight in pigeonpea (ICPL 227) inoculated with different rhizobial strains.

Rhizobial strain	Salinity level (dS/m) 0	4	6	8
		Nodule number (per pot)		
IC 3087	460	527 (115)	539 (118)	466 (102)
IC 3506	135	93 (70)	65 (50)	44 (34)
IC 3195	202	153 (76)	117 (58)	15 (8)
IC 3484	153	110 (72)	44 (29)	18 (12)
IC 3024	183	95 (52)	36 (20)	6 (3)
SE ± 7.7		LSD at 5% = 21.9		CV% = 9.4
SE ± 3.46 (for % of control)		LSD at 5%= 10.4		CV% = 10.4
		Total nodule dry matter (mg/pot)		
IC 3087	261	173 (65)	168 (64)	128 (49)
IC 3506	400	264 (66)	228 (57)	140 (35)
IC 3195	379	267 (71)	211 (56)	32 (8)
IC 3484	419	276 (66)	161 (39)	38 (9)
IC 3024	348	221 (64)	175 (50)	33 (9)
SE ± 14.8		LSD at 5% = 42.0		CV% = 13.8
SE ± 2.93 (for % of control)		LSD at 5% = 8.8		CV% = 9.5
		Average nodule weight (mg/nodule)		
IC 3087	0.57	0.33	0.31	0.28
IC 3506	3.12	2.89	3.60	3.16
IC 3195	1.88	1.74	1.82	2.20
IC 3484	2.78	2.53	3.65	2.07
IC 3024	1.90	2.33	4.99	5.48
SE ± 0.403		LSD at 5% = 1.21		CV% = 35.3

Note: Figures in parenthesis are '% of control'

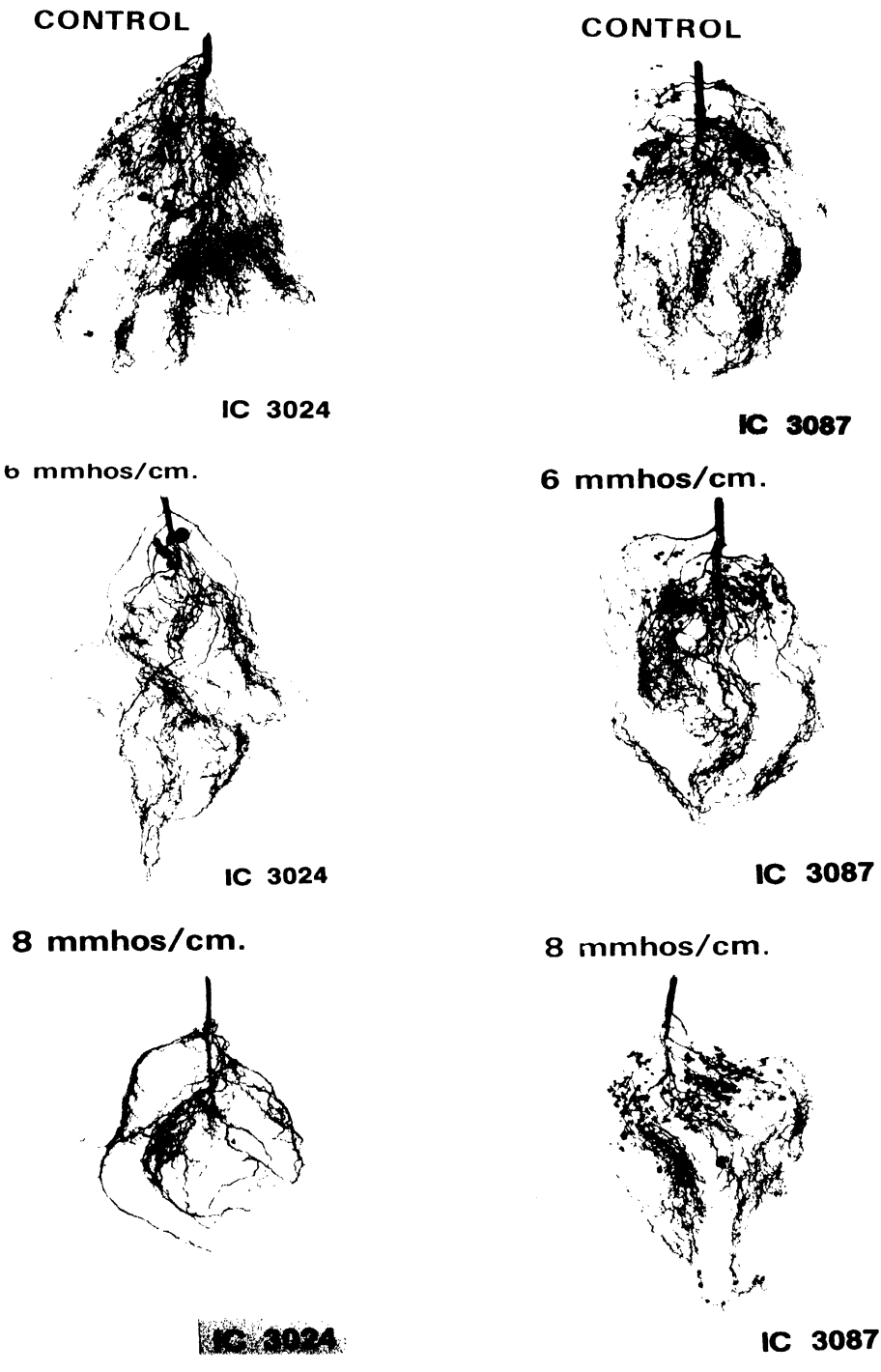

Plate 4. Effect of salinity on nodulation of pigeonpea inoculated with two different rhizobial strains IC 3024 and IC 3087, 65 days after sowing.

matter was significantly less affected than in others. At 6 dS/m, IC 3484 was significantly more affected than others. At 8 dS/m, IC 3506 and IC 3087 were less affected than the other three strains. Nodule dry matter decreased with increasing salinity in both early and late inoculated IC 3024 (Table 4.6.4). In the early inoculated treatment nodule dry matter was less affected at 8 dS/m compared to the late inoculated treatment.

4.6.4.3 Effect on the average nodule weight: Average nodule dry weight (mg/nodule) was significantly affected with increasing salinity (Table 4.6.3). The average nodule weight was highest in IC 3024 (3.68mg/nodule), and lowest in IC 3087 (0.37mg/nodule). In IC 3024, the average nodule weight increased with increasing salinity. In the other rhizobial strains, IC 3506, IC 3484, IC 3087 and IC 3195, there was no significant change in the average nodule weight. The average nodule weight was greater in the IC 3024 late inoculated treatment compared to the early inoculated (Table 4.6.4).

4.6.4.4 Effect on total nitrogenase activity: In all the rhizobial treatments, the total nitrogenese activity significantly decreased with increasing salinity. However, the such decrease was significantly less in IC 3087 than the others at the various salinity levels (Table 4.6.5). In the early inoculated treatment, the reduction in total nitrogenase activity was less than the late inoculated treatment at various salinity levels, but it was significant only at 8 dS/m salinity level (Table 4.6.4).

4.6.4.5 Effect on the specific nitrogenase activity: There was a

Table 4.6.4 Effect of time of inoculation with IC 3024 on nodule number and nodule dry matter, total and specific nitrogenase activity of pigeonpea genotype ICPL 227 at various salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8
		Nodule number (per pot)		
Early	176	120 (69)	106 (60)	77 (45)
Late	183	95 (52)	36 (20)	6 (3)
SE ± 7.7		LSD at 5% = 21.9		CV% = 9.4
SE ± 3.46 (for % of control)		LSD at 5%= 10.4		CV% = 10.4
		Total nodule dry matter (mg/pot)		
Early	307	200 (65)	177 (58)	149 (49)
Late	348	221 (64)	175 (50)	33 (9)
SE ± 14.8		LSD at 5% = 42.0		CV% = 13.8
SE ± 2.93 (for % of control)		LSD at 5%= 8.8		CV% = 9.5
		Average nodule weight (mg/nodule)		
Early	1.76	1.67	1.68	1.95
Late	1.90	2.33	4.99	5.48
SE ± 0.403		LSD at 5% = 1.21		CV% = 35.3
		Total nitrogenase activity (mmoles C2H4/pot/h)		
Early	52.3	21.5 (41.6)	19.3 (37)	18.5 (35.5)
Late	53.3	20.3 (38.7)	16.0 (30)	4.8 (9.0)
SE ± 1.83		LSD at 5% = 5.18		CV% = 16.3
SE ± 4.25 (for % of control)		LSD at 5%= 12.0		CV% =15.6
		Specific nitrogenase activity (mmoles C2H4/g nodule/h)		
Early	171	111	110	127
Late	156	92	92	174
SE ± 17.95		LSD at 5% = 50.8		CV% = 32.4

Note: Figures in parenthesis are '% of control'

Table 4.6.5. Effect of salinity on nitrogenase activity, leaf nitrogen and phosphorus (%) of pigeonpea genotype ICPL 227 inoculated with different rhizobial strains.

Rhizobial strain	Salinity level (dS/m) 0	4	6	8
	Total nitrogenase activity (mmoles C2H4/pot/h)			
IC 3087	24.0	18.3 (78)	14.3 (61)	12.5 (55)
IC 3506	45.8	22.0 (48)	20.5 (46)	15.5 (34)
IC 3195	38.3	19.0 (51)	17.5 (47)	5.5 (15)
IC 3484	45.0	18.0 (40)	15.3 (35)	4.3 (9)
IC 3024	53.3	20.3 (39)	16.0 (30)	4.8 (9)
SE ± 1.83		LSD at 5% = 5.2		CV% = 16.3
SE ± 4.25 (for % of control)		LSD at 5%= 12.02		CV% = 15.6
	Specific nitrogenase activity (mmoles C2H4/g nodule/h)			
IC 3087	91.7	105.5	86.4	97.6
IC 3506	115.6	84.8	90.7	114.6
IC 3195	101.3	71.8	83.6	192.9
IC 3484	109.3	66.5	97.1	114.6
IC 3024	155.7	91.7	92.4	174.2
SE ± 17.95		LSD at 5% = 50.8		CV% = 32.4
	Leaf nitrogen concentration (%)			
Nitrogen fed	3.20	3.20	3.62	4.01
IC 3087	3.19	3.20	3.23	3.39
IC 3506	3.20	3.25	3.30	3.49
IC 3195	3.31	3.32	3.28	2.55
IC 3484	3.30	2.95	2.93	2.92
IC 3024	3.25	2.85	2.44	2.45
SE ± 0.112		LSD at 5% = 0.324		CV% = 5.0
	Leaf phosphorus concentration (%)			
Nitrogen fed	0.15	0.15	0.18	0.26
IC 3087	0.15	0.15	0.17	0.22
IC 3506	0.16	0.16	0.16	0.24
IC 3195	0.15	0.17	0.19	0.28
IC 3484	0.16	0.15	0.17	0.24
IC 3024	0.15	0.16	0.18	0.26
SE ± 0.009		LSD at 5% = 0.026		CV% = 6.9

Note: Figures in parenthesis are '% of control'

significant effect of salinity on the specific nitrogenase activity (Table 4.6.5). In IC 3024, specific nitrogenase activity decreased at 4 and 6 dS/m. In IC 3506, IC 3484 and IC 3087, there was no significant change in the specific nitrogenase activity. In IC 3195, there was a significant increase at 8 dS/m salinity level. Specific nitrogenase activity was more affected by salinity in the late - inoculated IC 3024 treatment (Table 4.6.4).

4.6.4.6 Effect on the leaf nitrogen: In the N-fed treatment, leaf nitrogen (%) increased with salinity (Table 4.6.5). In IC 3024 and IC 3484, leaf nitrogen (%) decreased with increasing salinity. In IC 3195, this decrease was only at 8 dS/m. In IC 3506 and IC 3087, there was no significant change in the leaf nitrogen (%) with salinity. In IC 3024 late inoculation treatment, leaf nitrogen (%) decreased with increasing salinity, whereas in the early inoculated treatment, there was no significant change in the leaf nitrogen (%) with increasing salinity (Table 4.6.6)

4.6.4.7 Phosphorus: Leaf phosphorus levels (%) increased with increasing salinity in all the nitrogen treatments and there was no interaction between nitrogen treatments and salinity levels (Table 4.6.5). There were no differences in IC 3024 early and late inoculated treatments (Table 4.6.6).

4.6.4.8 Sodium: In all the nitrogen treatments leaf and stem sodium (%) increased with increasing salinity (Table 4.6.7). At 8 dS/m in IC 3024, IC 3484 and IC 3195 treatments shoot sodium was significantly higher than in N-fed, IC 3506 and IC 3087 treatments. At 8 dS/m, the

Table 4.6.6. Effect of time of inoculation of IC 3024 on leaf nitrogen, phosphorus, sodium, potassium and chloride content (%) of pigeonpea genotype ICPL 227 at various salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8
		Leaf nitrogen concentration (%)		
Early	3.15	3.14	3.05	3.28
Late	3.25	2.85	2.44	2.45
SE ± 0.112		LSD at 5% = 0.324		CV% = 5.0
		Leaf phosphorus concentration (%)		
Early	0.15	0.16	0.16	0.26
Late	0.15	0.16	0.18	0.26
SE ± 0.009		LSD at 5% = 0.026		CV% = 6.9
		Leaf sodium concentration (%)		
Early	0.03	0.15	0.19	0.30
Late	0.02	0.11	0.17	0.43
SE ± 0.032		LSD at 5% = 0.094		CV% = 31.8
		Leaf potassium concentration (%)		
Early	2.10	2.25	2.55	2.90
Late	2.15	2.25	2.25	2.25
SE ± 0.079		LSD at 5% = 0.228		CV% = 4.6
		Leaf chloride concentration (%)		
Early	0.05	1.38	2.59	3.92
Late	0.05	1.21	3.18	4.84
SE ± 0.065		LSD at 5% = 0.189		CV% = 4.4

Table 4.6.7. Effect of salinity on leaf, stem and root sodium (%) of pigeonpea genotype ICPL 227 inoculated with different rhizobial strains.

Rhizobial strain	Salinity level (dS/m) 0	4	6	8
	Leaf sodium concentration (%)			
IC 3087	0.02	0.02	0.04	0.15
IC 3506	0.02	0.20	0.21	0.18
IC 3195	0.03	0.07	0.15	0.40
IC 3484	0.03	0.07	0.09	0.37
IC 3024	0.02	0.11	0.17	0.43
Nitrogen fed	0.07	0.12	0.17	0.25
SE ± 0.033	LSD = 0.094		CV% = 31.8	
	Stem sodium concentration (%)			
IC 3087	0.04	0.12	0.12	0.29
IC 3506	0.04	0.17	0.17	0.19
IC 3195	0.04	0.13	0.16	0.55
IC 3484	0.04	0.12	0.28	0.70
IC 3024	0.04	0.05	0.28	0.61
Nitrogen fed	0.03	0.04	0.19	0.25
SE ± 0.0326	LSD = 0.095		CV% = 24.5	
	Root sodium concentration (%)			
IC 3087	0.56	1.13	1.50	1.60
IC 3506	0.56	1.20	1.25	1.60
IC 3195	0.60	1.31	1.55	1.85
IC 3484	0.65	1.25	1.70	1.85
IC 3024	0.70	1.20	1.64	1.78
Nitrogen fed	0.54	0.65	1.08	1.53
SE ± 0.083	LSD = 0.242		CV% = 9.6	

late inoculated IC 3024 treatment had significantly higher leaf sodium (%) than the early inoculated treatment (Table 4.6.6). Root sodium increased with increasing salinity in the medium in all the nitrogen treatments and there was no interaction between nitrogen treatment and salinity level (Table 4.6.7). There was no significant difference in the root sodium levels between early and late inoculated IC 3024 treatments (data not presented).

4.6.4.9 Chloride: The leaf, stem and root chloride (%) increased with salinity in all the nitrogen treatments (Table 4.6.8). In IC 3024, IC 3484, IC 3195 leaf chloride levels were significantly higher than in N-fed, IC 3506 and IC 3087 nitrogen treatments. Late inoculated IC 3024 treatment had significantly higher tissue chloride levels than the early inoculated treatment (Table 4.6.6) (data for stem and root chloride levels are not presented).

Table 4.6.8. Effect of salinity on leaf, stem and root chloride (%) of pigeonpea genotype ICPL 227 inoculated with different rhizobial strains.

Rhizobial strain	Salinity level (dS/m) 0	4	6	8
		Leaf chloride concentration (%)		
IC 3087	0.07	1.27	2.62	4.05
IC 3506	0.07	1.31	2.62	3.64
IC 3195	0.07	1.26	2.70	4.44
IC 3484	0.07	1.30	3.23	4.40
IC 3024	0.05	1.21	3.18	4.84
Nitrogen fed	0.06	1.41	2.43	3.92
SE ± 0.065		LSD = 0.189	CV% = 4.4	
		Stem chloride concentration (%)		
IC 3087	0.12	1.45	2.05	2.81
IC 3506	0.14	1.41	2.24	2.83
IC 3195	0.11	1.60	2.13	3.45
IC 3484	0.15	1.49	2.18	3.75
IC 3024	0.10	1.31	2.79	3.64
Nitrogen fed	1.13	1.58	2.06	2.67
SE ± 0.081		LSD = 0.236	CV% = 6.6	
		Root chloride concentration (%)		
IC 3087	0.60	2.20	2.40	2.40
IC 3506	0.60	2.25	2.15	2.25
IC 3195	0.60	2.10	2.20	2.50
IC 3484	0.70	1.95	2.25	2.65
IC 3024	0.70	2.20	2.40	2.70
Nitrogen fed	0.65	1.80	2.10	2.15
SE ± 0.098		LSD = 0.284	CV% = 7.4	

4.7A Response of Atylosia platycarpa - Rhizobium symbiosis to salinity.

This is essentially a continuation of the studies on the response of pigeonpea-Rhizobium symbiotic system to salinity stress. A wild species related to pigeonpea, A. platycarpa, was selected because of its high level of tolerance to salinity compared to the tolerant cultivated pigeonpea checks. Two Rhizobium strains, IC 3087 and IC 3484, which differ in their symbiotic effeciency under saline conditions with cultivated pigeonpea, were used in this study. There were three nitrogen treatments, nitrogen fed (N-fed), IC 3087 and IC 3484, and six salinity treatments, 0, 4, 6, 8, 10 and 12 dS/m. Salinity treatments were imposed on 14 day old seedlings. For the N-fed treatment, 50 ppm nitrogen as ammonium nitrate was supplied from 28 days after sowing. The experiment was conducted in a randomized complete block design replicated four times. Plants were harvested 65 days after sowing. The experimental conditions and other details were similar to the Experiment 4.6

4.7B Functioning of Atylosia platycarpa - Rhizobium symbiotic system under salinity in relation to time of inoculation.

The purpose of this study was to understand whether the early stages of establishment of the symbiotic system are more sensitive to salinity stress compared to the functioning of the symbiosis. The rhizobial treatments were IC 3087 early (inoculated at the time of sowing), IC 3087 late (inoculated 14 days after sowing), IC 3484 early, IC 3484 late and 6 salinity treatments, 0, 4, 6, 8, 10 and 12 dS/m. Salinity treatments were imposed on 14 day old

seedlings. This experiment was also conducted in a randomized complete block design, replicated four times. Plants were harvested 65 days after sowing.

Findings (4.7A and 4.7B)

Rhizobium strain IC 3087 formed an effective symbiosis with A. platycarpa within two weeks after inoculation, while IC 3484 was found non-infective. Hence the treatments involving IC 3484 were not included in the analysis. In the absence of salinity, i.e control, plant growth was good in both N-fed and Rhizobium inoculated treatments. At the various salinity treatments, plants grew better with late rhizobial inoculated IC 3087 than with early inoculation. These differences became more apparent with increasing salinity level in the medium. At 12 dS/m, all plants died in the early inoculated treatment and in the late inoculated IC 3087 treatment plants were pale green with nitrogen deficiency symptoms. Plants in N-fed treatment remained healthy at 12 dS/m.

4.7.1 Effect on leaf area: Leaf area was significantly decreased with increasing salinity (Table 4.7.1). However, the reduction was significantly more in the IC 3087 inoculated treatment than the N-fed. The early inoculated treatment suffered more reduction than the late inoculated treatment and this was significant at 8 and 10 dS/m salinity levels.

4.7.2 Effects on shoot dry matter: Shoot dry matter significantly decreased with increasing salinity in the N-fed as well as IC 3087

Table 4.7.1. Effect of salinity on leaf area, shoot, and pod dry weight of Rhizobium (IC 3087) inoculated and N-fed Atylosia platycarpa.

Nitrogen source	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf area (cm2/pot)			
IC 3087 early	306	234 (77)	156 (52)	84 (28)	40 (16)	28 (12)
IC 3087 late	263	189 (72)	173 (66)	119 (45)	109 (41)	43 (16)
Nitrogen fed	312	281 (90)	278 (88)	227 (74)	170 (55)	140 (45)
SE ± 15.4			LSD at 5% = 43.0		CV% = 16.9	
SE ± 4.96 (for '% of control')			LSD at 5% = 13.9		CV% = 16.4	
			Shoot dry weight (g/pot)			
IC 3087 early	7.03	5.06 (72)	3.81 (54)	2.60 (37)	1.78 (25)	1.64 (23)
IC 3087 late	4.26	3.36 (81)	2.85 (69)	2.25 (55)	2.06 (50)	1.19 (29)
Nitrogen fed	4.96	4.47 (91)	4.05 (82)	2.91 (59)	2.30 (47)	2.04 (41)
SE ± 0.176			LSD at 5% = 0.493		CV% = 9.8	
SE ± 3.62 (for '% of control')			LSD at 5% = 10.1		CV% = 11.6	
			Root dry weight (mg/pot)			
IC 3087 early	681	668 (99)	503 (74)	398 (58)	295 (44)	293 (44)
IC 3087 late	412	391 (95)	392 (95)	333 (82)	280 (69)	182 (44)
Nitrogen fed	690	655 (95)	627 (93)	514 (75)	398 (58)	352 (52)
SE ± 31.0			LSD at 5% = 86.8		CV% = 13.2	
SE ± 6.12 (for '% of control)			LSD at 5% = 17.14		CV% = 16.14	
			Pod dry weight (g/pot)			
IC 3087 early	3.70	2.51 (68)	1.77 (48)	1.09 (30)	0.55 (15)	0.43 (15)
IC 3087 late	1.70	1.43 (88)	1.09 (68)	0.77 (48)	0.63 (38)	0.28 (18)
Nitrogen fed	1.47	1.33 (90)	1.20 (81)	0.83 (56)	0.60 (41)	0.49 (33)
SE ± 0.120			LSD at 5% = 0.336		CV% = 16.4	
SE ± 4.94 (for '% of control)			LSD at 5% = 13.8		CV% = 16.6	

Note: Figures in parenthesis are '% of control'

inoculated plants (Table 4.7.1). The N-fed treatment was relatively less affected than IC 3087 and these differences were significant only at 6 and 12 d/S. The early inoculated inoculated treatment suffered more reduction in shoot dry matter than the late inoculated treatments.

4.7.3 Effects on root dry matter: Root dry matter also significantly decreased with increasing salinity in the N-fed and IC 3087 inoculated treatments (Table 4.7.1). There were no significant differences between these two treatments at any of the salinity levels. The reduction in root dry matter with salinity was significantly more in the early inoculated compared to late inoculated treatment.

4.7.4 Effects on pod dry weight: Pod dry weight significantly decreased with increasing salinity (Table 4.7.1) in the N-fed and IC 3087 inoculated treatment. There were no significant differences between N-fed and IC 3087 treatments at any salinity level. The reduction in pod dry weight was significantly more in the early inoculated than the late inoculated.

4.7.5 Effect of salinity on nodulation and nitrogen fixation:

4.7.5.1 Nodule number: Nodule number decreased with increasing salinity in the early inoculated treatment, whereas, nodule number increased with increasing salinity up to 10 dS/m in the late inoculated treatment. The differences between the late and early inoculated treatment were significant (Table 4.7.2).

Table 4.7.2 Effect of time of inoculation of Atylosia platycarpa with Rhizobium strain IC 3087 on nodulation and nitrogen fixation at different salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8	10	12
			Nodule number (per pot)			
Early	124	131 (107)	116 (94)	88 (72)	81 (66)	89 (72)
Late	131	157 (120)	164 (126)	162 (124)	183 (139)	118 (90)
SE ± 6.35			LSD at 5% = 18.3		CV% = 9.9	
SE ± 4.93 (for '% of control')			LSD at 5% = 14.2		CV% = 9.8	
			Total nodule dry weight (mg/pot)			
Early	167	124 (76)	93 (58)	72 (44)	40 (25)	40 (25)
Late	105	96 (93)	100 (97)	81 (80)	60 (58)	26 (24)
SE ± 7.75			LSD at 5% = 22.4		CV% = 18.5	
SE ± 6.64 (for '% of control')			LSD at 5% = 19.2		CV% = 20.5	
			Average nodule dry weight (mg/nodule)			
Early	1.36	0.94	0.81	0.83	0.49	0.45
Late	0.80	0.61	0.61	0.50	0.33	0.22
SE ± 0.074			LSD at 5% = 0.213		CV% = 22.3	
			Total nitrogenase activity (mM of C2H4/pot/h)			
Early	5.17	3.65 (72)	2.11 (41)	2.15 (42)	1.03 (20)	0.24 (5)
Late	5.29	3.85 (73)	2.38 (45)	2.27 (43)	1.05 (20)	1.05 (20)
SE ± 0.176			LSD at 5% = 0.51		CV% = 14.0	
SE ± 3.23 (for '% of control)			LSD at 5% = 9.30		CV% = 13.4	
			Specific nitrogenase activity (mM of C2H4/g nod dry wt/h)			
Early	32.2	30.3	23.1	31.4	26.8	6.3
Late	51.6	40.4	24.3	28.4	17.9	49.2
SE ± 5.87			LSD at 5% = 16.9		CV% = 38.9	

Note: Figures in parenthesis are '% of control'

4.7.5.2 Nodule dry weight: Nodule dry weight decreased with increasing salinity in both early and late inoculated treatments (Table 4.7.2). However, the early inoculated treatment was significantly, more affected than the late inoculated treatment. The average nodule dry weight also decreased with increasing salinity (Table 4.7.2) in the early and late inoculated treatments. The average nodule weight was significantly lower in the late inoculated treatment than the early inoculated treatment at each salinity level, including the control.

4.7.5.3 Effect on the total and specific nitrogenase activity: Total (mM of C2H4/pot/h) and specific (mM of C2H4/g/nod) nitrogenase activity decreased with increasing salinity in both early and late inoculated treatments (Table 4.7.2). There were no significant differences betwen the late and early inoculation treatments.

4.7.5.4 Effect on tissue nitrogen concentration: Leaf, pod, stem and root nitrogen (%) was significantly affected by salinity (Table 4.7.3). In the N-fed treatment leaf nitrogen (%) increased with salinity, and in the IC 3087 treatment it decreased with salinity. Pod nitrogen levels increased with salinity in both N-fed and IC 3087 treatments. Stem and root nitrogen levels increased with salinity in N-fed and in IC 3087 there was no significant change. In the early inoculated IC 3087 treatment there was no significant change in the leaf nitrogen (%) with increasing salinity, and in late inoculated treatment, there was a decrease with increasing salinity. In the pod nitrogen levels, there was no significant change with salinity in the early inoculated treatment whereas there was an

Table 4.7.3. Effect of salinity on pod, stem, and root nitrogen (%) of Rhizobium (IC 3087) inoculated and N-fed Atylosia platycarpa.

Nitrogen source	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf nitrogen concentration (%)			
IC 3087 early	2.93	2.79	2.55	2.84	2.39	2.48
IC 3087 late	3.61	3.31	3.25	2.96	2.75	2.54
Nitrogen fed	2.28	3.10	3.54	4.52	4.62	4.59
SE ± 0.269			LSD at 5% = 0.787		CV% = 11.8	
			Pod nitrogen concentration (%)			
IC 3087 early	2.34	2.51	2.52	2.71	2.96	2.78
IC 3087 late	2.61	2.71	2.81	2.86	2.80	3.29
Nitrogen fed	2.08	2.24	2.30	3.06	3.49	3.54
SE ± 0.148			LSD at 5% = 0.434		CV% = 7.7	
			Stem nitrogen concentration (%)			
IC 3087 early	1.07	1.13	1.17	1.17	1.31	1.58
IC 3087 late	1.42	1.33	1.40	1.46	1.35	1.60
Nitrogen fed	1.41	1.28	1.56	2.19	2.48	2.60
SE ± 0.096			LSD at 5% = 0.281		CV% = 8.6	
			Root nitrogen concentration (%)			
IC 3087 early	1.86	1.78	1.82	1.83	1.85	2.01
IC 3087 late	2.01	2.02	2.01	2.23	2.04	2.00
Nitrogen fed	1.68	1.86	1.96	2.20	2.12	2.63
SE ± 0.093			LSD at 5% = 0.272		CV% = 6.8	

increase in the late inoculated treatment. The stem nitrogen levels significantly increased only in the early inoculated treatment. There was no significant change in root nitrogen levels in the early and late inoculated treatments with salinity.

4.7.6 Effects on leaf, pod, stem, and root phosphorus (%): The phosphorus (%) levels in leaf, pod, stem and root were significantly affected with increasing salinity (Table 4.7.4). There was a significant increase in the leaf phosphorus (%) with salinity in the N-fed treatment and not in the IC 3087 treatment. In stem and pod, the phosphorus content increased with salinity in both N-fed and IC 3087 treatments. In root, the phosphorus content increased with salinity only in the IC 3087 treatment and not the N-fed treatment. There was no significant change in the leaf phosphorus (%) in the early and late inoculated treatments with increasing salinity. Pod, stem and root phosphorus increased significantly with increasing salinity in both early and late inoculated IC 3087 treatments (data not presented).

4.7.7 Effects on tissue sodium concentration: Leaf sodium (%) increased with increasing salinity particularly in IC 3087 treatment at 12 dS/m (Table 4.7.5). There was no effect of salinity on pod sodium levels in both N-fed and IC 3087 treatments. The stem and root sodium levels increased with salinity and this was significantly higher in the IC 3087 treatment than the N-fed treatment.

inoculated and N-fed Atylosia platycarpa.

Nitrogen source	Salinity level (dS/m)					
	0	4	6	8	10	12
	Leaf phosphorus concentration (%)					
IC 3087	0.18	0.16	0.16	0.19	0.18	0.20
Nitrogen fed	0.16	0.18	0.22	0.24	0.25	0.27
SE ± 0.016			LSD at 5% = 0.047			CV% = 12.3
	Pod phosphorus concentration (%)					
IC 3087	0.22	0.22	0.24	0.26	0.26	0.34
Nitrogen fed	0.23	0.23	0.26	0.29	0.31	0.32
SE ± 0.019			LSD at 5% = 0.055			CV% = 10.5
	Stem phosphorus concentration (%)					
IC 3087	0.12	0.10	0.11	0.14	0.13	0.20
Nitrogen fed	0.14	0.14	0.18	0.19	0.24	0.25
SE ± 0.0182			LSD at 5% = 0.053			CV% = 17.6
	Root phosphorus concentration (%)					
IC 3087	0.08	0.07	0.09	0.12	0.10	0.13
Nitrogen fed	0.12	0.11	0.12	0.12	0.12	0.12
SE ± 0.0076			LSD at 5% = 0.022			CV% = 11.7

Table 4.7.5. Effect of salinity on leaf, pod, stem, and root sodium (%) of Rhizobium (IC 3087) inoculated and N-fed Atylosia platycarpa.

Nitrogen source	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf sodium concentration (%)			
IC 3087	0.05	0.05	0.05	0.07	0.06	0.13
Nitrogen fed	0.05	0.05	0.06	0.07	0.06	0.08
SE ± 0.012			LSD at 5% = 0.0353			CV% = 21.4
			Pod sodium concentration (%)			
IC 3087	0.03	0.01	0.03	0.03	0.05	0.09
Nitrogen fed	0.04	0.04	0.04	0.04	0.04	0.05
SE ± 0.0151			LSD at 5% = 0.044			CV% = 56.6
			Stem sodium concentration (%)			
IC 3087	0.08	0.10	0.13	0.27	0.30	0.72
Nitrogen fed	0.14	0.15	0.22	0.27	0.30	0.30
SE ± 0.055			LSD at 5% = 0.162			CV% = 28.2
			Root sodium concentration (%)			
IC 3087	0.91	2.12	2.32	2.62	2.60	2.50
Nitrogen fed	0.54	2.46	2.50	2.60	2.50	2.45
SE ± 0.168			LSD at 5% = 0.49			CV% = 11.3

Table 4.7.6 Effect of time of inoculation of Atylosia platycarpa with Rhizobium IC 3087 on leaf sodium concentration (%) at different salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf sodium concentration (%)			
Early	0.07	0.07	0.07	0.05	0.11	0.23
Late	0.05	0.05	0.05	0.07	0.06	0.13
SE ± 0.012			LSD at 5% = 0.0353			CV% = 21.4

In the early inoculated treatment, leaf sodium (%) was significantly higher than in the late inoculated treatment at 10 and 12 dS/m salinity levels (Table 4.7.6). There was no significant change in pod sodium level with salinity in both the early and late inoculated treatments. The stem and root sodium levels increased with salinity in both early and late inoculated treatments and there were no significant difference between them (data not presented for pod, stem and root sodium).

4.7.8 Potassium: Leaf, pod, stem and root potassium (%) increased with increasing salinity in the N-fed and IC 3087 treatments (Table 4.7.7). Only at 12 dS/m was the potassium concentration of leaf, pod and stem was significantly higher in the IC 3087 than the N-fed treatment. There were no significant differences in root potassium (%), between N-fed and IC 3087 treatments at any of the salinity levels. The potassium content in leaf, pod, stem and root increased with increasing salinity in the medium in the early and late inoculated treatments and there were no significant difference between them (data not presented).

4.7.9 Chloride: Leaf, pod, stem and root chloride (%) increased with increasing salinity in the N-fed and IC 3087 treatments (Table 4.7.8). In the N-fed treatment, the leaf chloride was significantly higher than in the IC 3087 treatment at the different salinity levels. There was no significant differences in the pod, stem and root chloride levels (%), between nitrogen fed and IC 3087 treatments at any of the salinity levels.

Table 4.7.7. Effect of salinity on leaf, pod, stem, and root potassium (%) of Rhizobium (IC 3087) inoculated and N-fed A. platycarpa.

Nitrogen source	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf potassium concentration (%)			
IC 3087	0.87	0.80	0.90	0.87	0.94	1.20
Nitrogen fed	0.68	0.83	0.88	0.93	0.92	0.90
SE ± 0.054			LSD at 5% = 0.159			CV% = 9.8
			Pod potassium concentration (%)			
IC 3087	1.34	1.64	1.70	1.88	1.85	2.00
Nitrogen fed	1.39	1.58	1.68	1.81	1.70	1.84
SE ± 0.0537			LSD at 5% = 0.157			CV% = 4.8
			Stem potassium concentration (%)			
IC 3087	1.46	1.52	1.71	1.88	1.81	2.08
Nitrogen fed	1.10	1.45	1.69	1.63	1.61	1.67
SE ± 0.080			LSD at 5% = 0.233			CV% = 7.7
			Root potassium concentration (%)			
IC 3087	1.20	1.60	1.80	1.80	1.90	1.70
Nitrogen fed	1.20	1.40	1.60	1.60	1.65	1.50
SE ± 0.134			LSD at 5% = 0.39			CV% = 13.2

Table 4.7.8. Effect of salinity on leaf, pod, stem, and root chloride (%) of Rhizobium (IC 3087) inoculated and N-fed A. platycarpa.

Nitrogen source	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf chloride concentration (%)			
IC 3087	0.12	1.75	2.70	3.60	3.34	4.21
Nitrogen fed	0.12	2.56	4.09	4.60	4.61	4.62
SE ± 0.186		LSD at 5% = 0.55			CV% = 8.3	
			Pod chloride concentration (%)			
IC 3087	0.19	0.75	1.04	1.27	1.24	1.68
Nitrogen fed	0.10	0.68	1.11	1.72	1.57	1.68
SE ± 0.137		LSD at 5% = 0.40			CV% = 18.1	
			Stem chloride concentration (%)			
IC 3087	0.20	1.27	1.63	1.83	1.98	2.96
Nitrogen fed	0.14	1.52	2.19	2.78	2.42	2.80
SE ± 0.176			LSD at 5% = 0.513			CV% = 12.8
			Root chloride concentration (%)			
IC 3087	0.28	2.50	2.80	3.00	3.20	3.30
Nitrogen fed	0.43	2.90	3.20	3.40	3.40	3.30
SE ± 0.124		LSD at 5% = 0.360			CV% = 7.1	

Table 4.7.9 Effect of time of inoculation of Atylosia platycarpa with Rhizobium (IC 3087) on leaf chloride concentration (%) at different salinity levels.

Time of inoculation	Salinity level (dS/m) 0	4	6	8	10	12
			Leaf chloride concentration (%)			
Early	0.15	2.75	3.64	4.16	4.81	5.16
Late	0.12	1.75	2.70	3.60	3.34	4.21
SE ± 0.186			LSD at 5% = 0.55			CV% = 8.3

Leaf, pod, stem and root chloride (%) increased with increasing salinity in the early and late inoculated IC 3087 treatments (Table 4.7.9). In the early inoculated treatment, leaf chloride were significantly higher than in the late inoculated treatment at the different salinity levels. There were no significant differences in pod, stem, and root chloride (%), between early and late inoculated treatments at any of the salinity levels (data not presented).

4.8 Inheritance of salinity tolerance.

From the earlier experiments, A. albicans was found to be one of the most tolerant species to salinity among all the cultivated or wild types of pigeonpea and far more efficient in ion regulation compared to the sensitive types. In order to understand the nature of inheritance of salinity tolerance, F1 hybrids obtained from the reciprocal crosses of Atylosia albicans (tolerant partner) and ICP 3783 (sensitive partner) were grown for 75 days at various levels of salinity (0, 6, 8, 10 and 12 dS/m). It was also intended to understand the specific physiological traits conferring salinity tolerance (eg. efficient sodium and chloride regulation, the ability to maintain high levels of potassium at high levels of salinity, etc.) and to determine whether these specific physiological traits are genetically controlled and to ascertain whether these traits are dominant. The experiment was laid out as randomized complete block design and replicated four times.

Findings

The results showed that the plants of Atylosia albicans could grow even at 12 dS/m (plate. 5), although there was a general decline in growth beyond a salinity level of 8 dS/m. In a few cases burning symptoms appeared on primary leaves only. In the cultivated pigeonpea, ICP 3783, salt burning symptoms were visible even at 6 dS/m salinity level, where plants mostly had weak stems (Plate. 5.). At 8 dS/m, these symptoms became very severe when growth was severely retarded and wilting started in a number of plants. At 10 and 12 dS/m, all the plants of ICP 3783 plants died.

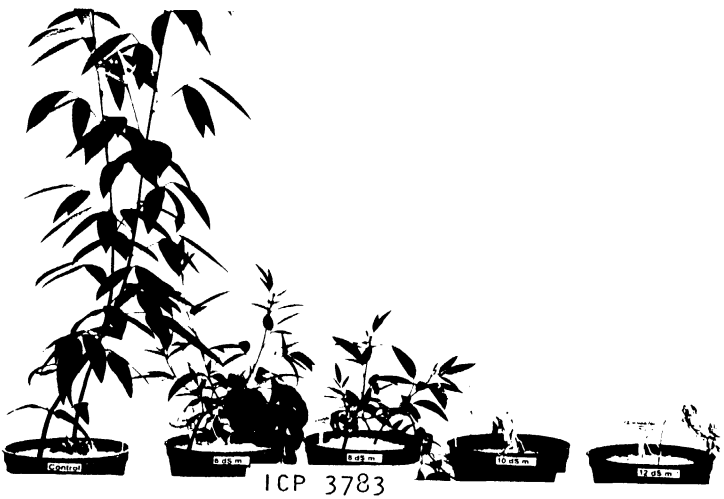

Plate 5. Growth response of Atylosia albicans, ICP 3783 and their F1 hybrid to different levels of salinity, 75 days after sowing.

The F1 hybrids of the cross A. albicans X ICP 3783, and their reciprocal were morphologically intermediate between both parents. The leaf shape was similar to A. albicans and the growth habit was intermediate, i.e neither twining like A. albicans nor erect like pigeonpea. The plants were healthy and able to grow up to 12 dS/m, without salt toxicity symptoms (Plate. 5), however, growth was affected.

4.8.1 Effects on leaf area: Leaf area was significantly affected with increasing salinity (Table 4.8.1 and Fig 4.8.1). The reduction in leaf area with salinity was far greater in ICP 3783 than A. albicans, and F1 hybrids. The response of F1 hybrids was similar to A. albicans and there was no significant difference between A. albicans and the F1 hybrids at any salinity level. There was no significant difference in leaf area between F1 reciprocals at any of the salinity levels, indicating that there was no maternal effect.

4.8.2 Effect on shoot and root dry matter: There was a decrease in shoot and root dry matter with increasing salinity (Table 4.8.1 and Fig 4.8.1). The reduction in shoot and root dry matter with increasing salinity was very high in ICP 3783 compared to A. albicans and their hybrids. There were no significant differences between A. albicans and the hybrids.

4.8.3 Effects on transpiration rate: Transpiration rate (mg/cm2/S) was observed to be affected by 10 days after salinity treatments were imposed (Table 4.8.2). In ICP 3783, leaf transpiration rate was severely affected with increasing salinity, resulting in an 80%

Table 4.8.1. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf area, shoot and root dry matter.

Genotype	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf area (cm2/plant)		
A. albicans	440	377 (87)	343 (79)	284 (66)	171 (39)
ICP 3783	839	379 (45)	226 (27)	69 (8)	0 (0)
A. albicans X ICP 3783	583	513 (88)	489 (84)	401 (69)	277 (48)
ICP 3783 X A. albicans	539	484 (90)	430 (80)	374 (70)	272 (50)
SE ± 23.4		LSD at 5% = 66.2		CV = 12.5%	
SE ± 3.05 (for % of control)		LSD at 5% = 8.6		CV = 9.2%	
			Shoot dry matter (mg/plant)		
A. albicans	2793	2339 (80)	1993 (72)	1527 (55)	968 (35)
ICP 3783	8037	3394 (42)	1847 (23)	796 (10)	315 (4)
A. albicans X ICP 3783	3775	3251 (86)	2996 (81)	2225 (60)	1684 (45)
ICP 3783 X A. albicans	3736	3076 (85)	3063 (81)	2386 (64)	1790 (48)
SE ± 276.2		LSD at 5% = 781		CV = 21.2%	
SE ± 3.71 (for % of control)		LSD at 5% = 10.5		CV = 11.7%	
			Root dry matter (mg/plant)		
A. albicans	745	587 (79)	532 (72)	369 (50)	261 (35)
ICP 3783	3425	1113 (33)	520 (15)	202 (6)	57 (2)
A. albicans X ICP 3783	1116	867 (79)	847 (77)	674 (60)	485 (43)
ICP 3783 X A. albicans	1335	1062 (80)	970 (73)	833 (63)	599 (46)
SE ± 83.5		LSD at 5% = 236		CV = 20.1%	
SE ± 4.21 (for % of control)		LSD at 5% = 11.89		CV = 13.9	

Note: Figures in parenthesis are '% of control'

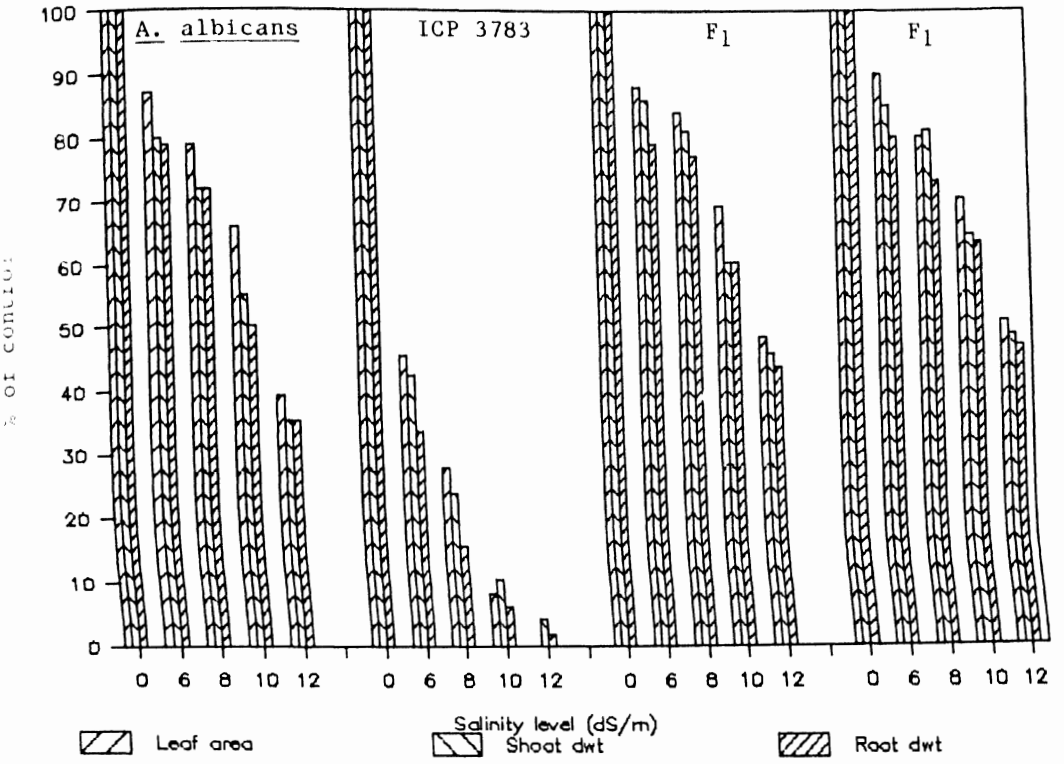

Fig. 4.8.1. Effect of salinity on plant growth of A. albicans (tolerant), ICP 3783 (sensitive) and their F_1 hybrids (A. albicans x ICP 3783 and ICP 3783 x A. albicans).

Table 4.8.2. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf transpiration rate (mg/cm2/S).
(Leaf transpiration measurements were taken ten and forty days after imposing salinity treatments)

Genotype	Salinity treatment (dS/m)				
	0	6	8	10	12
			Ten days after		
A. albicans	13.10	13.07	11.41	8.55	8.08
ICP 3783	15.51	11.69	9.64	3.06	1.19
A. albicans X ICP 3783	13.73	15.67	11.78	9.22	12.26
ICP 3783 X A. albicans	15.89	13.20	10.19	12.04	7.85
SE ± 1.248		LSD at 5% = 3.49		CV = 23.7%	
			Forty days after		
A. albicans	9.00	8.59	6.09	8.13	8.85
ICP 3783	10.52	2.89	1.15	0.32	0.00
A. albicans X ICP 3783	11.74	8.93	7.53	8.80	5.31
ICP 3783 X A. albicans	12.67	8.64	7.46	6.60	6.41
SE ± 0.990		LSD at 5% = 2.77		CV = 32.5%	

decrease at 10 and 12 dS/m salinity levels. In A. albicans, this decrease was not significant up to 8 dS/m, but at 10 and 12 dS/m salinity levels, there was significant decrease in the transpiration. Transpiration in A. albicans was comparatively less affected than ICP 3783. In the hybrids, there was generally no significant reduction in leaf transpiration rate with increasing salinity.

By 40 days after imposing salinity treatments, leaf transpiration rate showed considerable decrease with salinity (Table 4.8.2). In ICP 3783, leaf transpiration was severely affected at all salinity levels and at 8 dS/m and above transpiration was virtually stopped. In A. albicans, increasing salinity did not have any significant effect on the leaf transpiration rate. In the F1 hybrids, transpiration rate showed a decrease with increasing salinity, but this decrease was significant only at 6 dS/m salinity level and there was no further significant change in transpiration rate with increasing salinity. The differences between F1 hybrids in the transpiration rate at any of the salinity levels was not significant.

4.8.4 Ionic relations:

4.8.4.1 Sodium: The percentage of leaf sodium increased with increasing salinity (Table 4.8.3 and Fig 4.8.2). There were significant differences among types in the leaf sodium levels. Pigeonpea genotype ICP 3783 had the highest leaf sodium (average of 1.51%), whereas it was only 0.073% in A. albicans. The interaction between salinity level and types in leaf sodium was significant. The increase in leaf sodium was about 30 to 40 times and higher in ICP

Table 4.8.3. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root sodium (%).

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf sodium concentration (%)		
A. albicans	0.055	0.075	0.085	0.060	0.090
ICP 3783	0.095	0.190	1.185	2.320	3.735
A. albicans X ICP 3783	0.110	0.100	0.160	0.095	0.120
ICP 3783 X A. albicans	0.095	0.080	0.105	0.130	0.085
SE ± 0.0598		LSD at 5% = 0.177		CV = 18.9%	
			Stem sodium concentration (%)		
A. albicans	0.09	0.08	0.07	0.07	0.11
ICP 3783	0.09	0.65	1.95	2.71	4.18
A. albicans X ICP 3783	0.08	0.22	0.11	0.22	0.29
ICP 3783 X A. albicans	0.06	0.17	0.13	0.11	0.20
SE ± 0.0463		LSD at 5% = 0.137		CV = 11.3%	
			Root sodium concentration (%)		
A. albicans	0.58	1.95	2.29	2.26	2.09
ICP 3783	0.46	2.89	2.35	1.57	1.14
A. albicans X ICP 3783	0.65	1.72	2.17	2.69	2.74
ICP 3783 X A. albicans	0.64	1.98	2.47	2.58	2.75
SE ± 0.155		LSD at 5% = 0.457		CV = 11.5%	

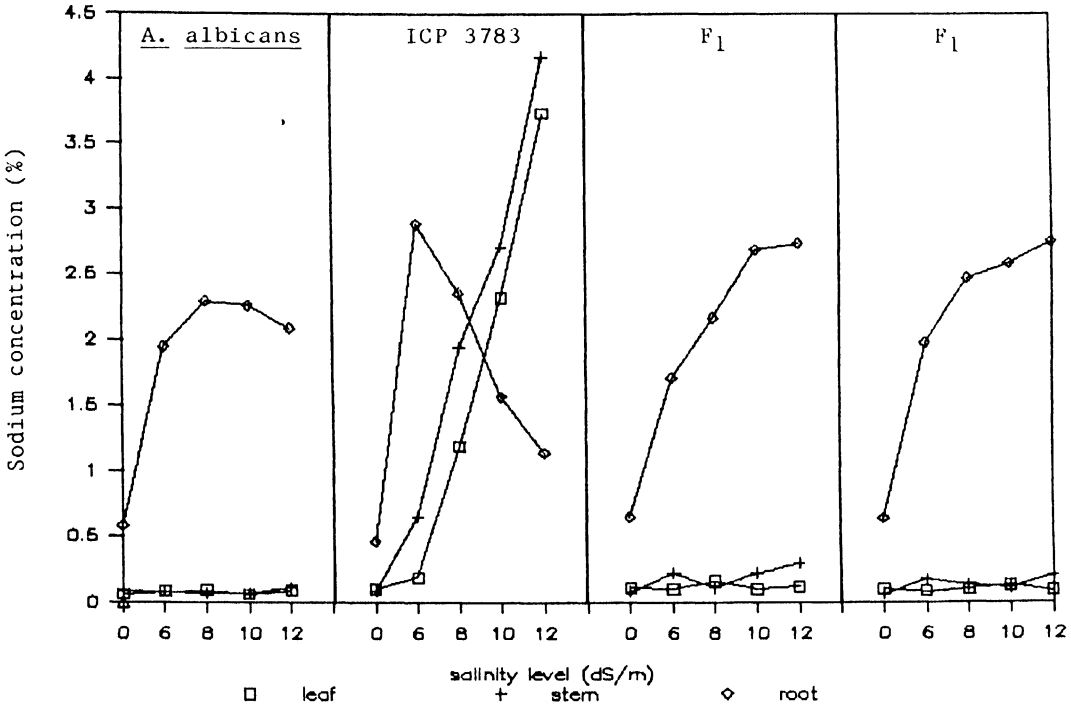

Fig. 4.8.2. Effect of salinity on tissue sodium concentration of A. albicans (tolerant), ICP 3783 (sensitive) and their F_1 hybrids (A. albicans x ICP 3783 and ICP 3783 x A. albicans).

3783 at all salinity levels than A. albicans or the F1 hybrids where there was no significant increase in the leaf sodium with salinity. The differences in the leaf sodium among A. albicans and F1 hybrids were not significant at any salinity level. This indicates that the physiological trait 'efficient sodium regulation (exclusion) capacity' was uniformly expressed in these F1 hybrids as in one of its parents, Atylosia albicans.

The stem sodium percentage also increased with increasing salinity (Table 4.8.3 and Fig 4.8.2). The differences among types and the interaction between type and salinity level was significant. ICP 3783 had the highest stem sodium with an average of 1.91%, whereas the amount was 0.08% in A. albicans. The increase in stem sodium was about 40 to 50 times higher in ICP 3783 as compared to A. albicans or the F1 hybrids at all salinity levels.

Root sodium percentage was also significantly increased with increasing salinity (Table 4.8.3 and Fig 4.8.2). The root sodium was lowest in ICP 3783 with an average of 1.68%, and highest in one of the F1 hybrids with an average of 2.08%. The interaction between salinity treatment and type was significant. In ICP 3783, the increase in root sodium was at 6 dS/m, and then declined at 8, 10, and 12 dS/m. In A. albicans, the increase was noticed up to 8 dS/m, and there was no further increase in root sodium at 10 and 12 dS/m.. In the F1 hybrids, root sodium increased with increasing salinity up to 12 dS/m. However, the differences among A. albicans, and the F1 hybrids in their root sodium levels were not significant at any of the salinity levels. This indicates that the higher sodium holding capacity of the roots was expressed in the F1 hybrids to the same extent as in parent

A. albicans.

4.8.5.2 Potassium: In ICP 3783, leaf potassium increased only at 6 dS/m and ,then declined at higher salinity levels (Table 4.8.4 and Fig 4.8.3). In A. albicans and the F1 hybrids, leaf potassium increased with increasing salinity up to 12 dS/m. There were no significant difference among A. albicans and the F1 hybrids in leaf potassium. Root potassium in ICP 3783 increased up to 8 dS/m, and then declined at 10 and 12 dS/m. In A. albicans as well as in their F1 hybrids the root potassium content increased at all salinity levels and their was little difference between the F1 hybrids and A. albicans.

4.8.4.3 Potassium/sodium ratio: The K/Na ratio in the leaf was significantly affected by increasing salinity. (Table 4.8.5). The average leaf K/Na ratio was highest in A. albicans (17.08) and lowest in ICP 3783 (3.66). In A. albicans, and the F1 hybrids, the K/Na ratio in the leaves increased with salinity, whereas there was a decrease in ICP 3783. The K/Na in A. albicans stem increased with increasing salinity whereas in ICP 3783 the K/Na ratio decreased with increasing salinity. The ratio of K/Na in the root decreased generally with increasing salinity (Table 4.8.5).

4.8.5.4 Calcium: The calcium concentration in the leaf, stem and root increased with increasing salinity (Table 4.8.6) in the parents and hybrids. The interaction between salinity level and types was significant.

Table 4.8.4. Response of *Atylosia albicans*, *Cajanus cajan* (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root potassium (%).

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf potassium concentration (%)		
A. albicans	0.74	1.06	1.19	1.50	1.62
ICP 3783	0.79	1.50	1.50	1.20	1.30
A. albicans X ICP 3783	0.88	1.26	1.28	1.55	1.65
ICP 3783 X *A. albicans*	1.04	1.23	1.42	1.41	1.74
SE ± 0.0682		LSD at 5% = 0.202		CV = 7.5%	
			Stem potassium concentration (%)		
A. albicans	1.07	1.66	1.68	1.86	2.14
ICP 3783	0.75	1.69	1.17	0.90	0.66
A. albicans X ICP 3783	0.87	1.50	1.42	2.08	2.13
ICP 3783 X *A. albicans*	1.11	1.46	1.57	1.57	1.84
SE ± 0.0835		LSD at 5% = 0.247		CV = 8.1%	
			Root potassium concentration (%)		
A. albicans	1.02	1.06	1.17	1.19	1.35
ICP 3783	0.73	1.40	1.72	0.78	0.42
A. albicans X ICP 3783	0.83	0.83	0.85	1.23	1.39
ICP 3783 X *A. albicans*	1.11	1.17	1.07	1.07	1.26
SE ± 0.119		LSD at 5% = 0.353		CV = 15.6%	

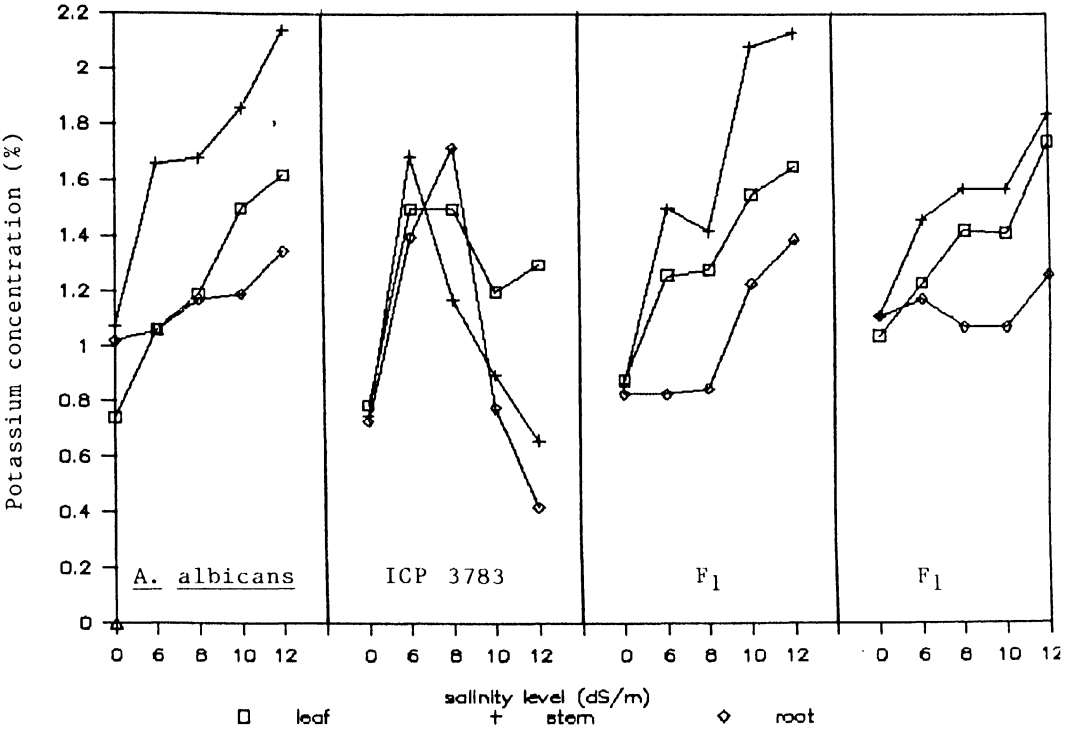

Fig. 4.8.3. Effect of salinity on tissue potassium concentration (%) of A. albicans (tolerant), ICP 3783 (sensitive) and their F_1 hybrids (A. albicans x ICP 3783 and ICP 3783 x A. albicans).

Table 4.8.5. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root potassium/sodium ratio.

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf potassium/sodium ratio		
A. albicans	13.6	14.6	14.1	24.9	18.2
ICP 3783	8.3	7.9	1.3	0.5	0.4
A. albicans X ICP 3783	8.1	12.7	8.0	16.7	15.9
ICP 3783 X A. albicans	11.0	16.0	13.5	11.3	20.4
SE ± 2.11		LSD at 5% = 6.24		CV = 25.1%	
			Stem potassium/sodium ratio		
A. albicans	11.9	24.0	30.0	28.8	19.9
ICP 3783	9.1	2.8	0.6	0.3	0.2
A. albicans X ICP 3783	12.2	7.1	13.2	10.9	7.8
ICP 3783 X A. albicans	19.3	9.0	12.1	14.3	9.4
SE ± 4.10		LSD at 5% = 12.1		CV = 47.8%	
			Root potassium/sodium ratio		
A. albicans	1.75	0.54	0.51	0.53	0.64
ICP 3783	1.57	0.48	0.74	0.50	0.37
A. albicans X ICP 3783	1.28	0.48	0.39	0.46	0.50
ICP 3783 X A. albicans	1.72	0.59	0.43	0.41	0.45
SE ± 0.0635		LSD at 5% = 0.188		CV = 12.5%	

Table 4.8.6 Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root calcium (%).

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf calcium concentration (%)		
A. albicans	2.95	3.19	3.88	3.64	3.40
ICP 3783	2.44	3.87	3.70	3.83	3.51
A. albicans X ICP 3783	2.37	2.73	3.19	3.32	3.66
ICP 3783 X A. albicans	2.66	2.75	2.89	3.05	3.57
SE ± 0.159		LSD at 5% = 0.47		CV = 7.0%	
			Stem calcium concentration (%)		
A. albicans	1.89	2.56	2.42	2.77	3.04
ICP 3783	2.25	2.41	1.93	2.11	3.35
A. albicans X ICP 3783	1.84	2.67	2.44	2.67	2.61
ICP 3783 X A. albicans	2.02	2.02	2.30	2.35	2.35
SE ± 0.173		LSD at 5% = 0.510		CV = 10.2%	
			Root calcium concentration (%)		
A. albicans	1.00	1.08	1.38	1.29	1.20
ICP 3783	0.51	0.45	0.45	0.67	0.83
A. albicans X ICP 3783	1.16	1.33	1.12	1.41	1.18
ICP 3783 X A. albicans	1.10	1.26	1.35	1.30	0.45
SE ± 0.08		LSD at 5% = 0.236		CV = 11.0%	

4.8.4.5 Magnesium: Leaf magnesium levels were significantly affected by increasing salinity (Table 4.8.7). The interaction between salinity treatment and type was significant. The magnesium concentration in the stem increased with salinity in all types (Table 4.8.7). Root magnesium decreased with increasing salinity in the medium in all the types (Table 4.8.7). There was no significant interaction between salinity level and types in root magnesium levels.

4.8.5.6 Chloride: Leaf chloride increased with increasing salinity in all the types (Table 4.8.8 and Fig 4.8.4). The increase in leaf chloride was very high extending from 0.15% in the control to 7.85% at 12 dS/m salinity level in ICP 3783. In A. albicans, this increase was only from 0.13% in the control to 2.6% at 12 dS/m. There was no significant difference among A. albicans, and its F1 hybrids in relation to leaf chloride content. Thus it appeared that this physiological trait of efficient chloride regulation capacity was expressed equally in A. albicans and the F1 hybrids. The stem chloride levels also showed an increase with increasing salinity in both the parents and F1 hybrids. The trends were similar with respect to leaf chloride.

Root chloride was also significantly affected with increasing salinity (Table 4.8.8 and Fig 4.8.4). In ICP 3783, root chloride increased at 6 dS/m and then declined at higher salinity levels. In A. albicans and the F1 hybrids, root chloride increased with increasing salinity up to 12 dS/m. The higher chloride retention capacity of the root was similar to that of A. albicans and its F1 hybrids.

Table 4.8.7. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root magnesium (%).

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf magnesium concentration (%)		
A. albicans	0.16	0.14	0.15	0.14	0.17
ICP 3783	0.27	0.26	0.22	0.25	0.34
A. albicans X ICP 3783	0.23	0.16	0.15	0.15	0.14
ICP 3783 X A. albicans	0.17	0.14	0.15	0.14	0.16
SE ± 0.015	LSD at 5% = 0.043			CV = 11.3%	
			Stem magnesium concentration (%)		
A. albicans	0.093	0.145	0.151	0.151	0.183
ICP 3783	0.121	0.149	0.160	0.167	0.213
A. albicans X ICP 3783	0.113	0.160	0.170	0.180	0.171
ICP 3783 X A. albicans	0.125	0.113	0.157	0.141	0.166
SE ± 0.012		LSD at 5% = 0.012		CV = 11.4%	
			Root magnesium concentration (%)		
A. albicans	1.32	0.69	0.65	0.75	0.46
ICP 3783	0.60	0.59	0.65	0.59	0.39
A. albicans X ICP 3783	1.10	0.53	0.54	0.65	0.59
ICP 3783 X A. albicans	1.40	0.74	0.64	0.59	0.58
SE ± 0.112		LSD at 5% = 0.33		CV = 22.5%	

Table 4.8.8 Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, stem and root chloride (%).

Genotypes	Salinity treatment (dS/m)				
	0	6	8	10	12
	Leaf chloride concentration (%)				
A. albicans	0.13	1.34	1.66	2.14	2.60
ICP 3783	0.15	4.00	5.52	6.11	7.85
A. albicans X ICP 3783	0.17	1.21	1.62	2.33	2.79
ICP 3783 X A. albicans	0.18	1.09	1.60	2.00	2.68
SE ± 0.148		LSD at 5% = 0.439		CV = 8.9%	
	Stem chloride concentration (%)				
A. albicans	0.15	1.32	1.57	1.68	2.07
ICP 3783	0.30	2.37	3.08	4.42	4.75
A. albicans X ICP 3783	0.15	1.39	1.57	2.00	2.23
ICP 3783 X A. albicans	0.16	1.15	1.62	1.61	1.94
SE ± 0.076		LSD at 5% = 0.225		CV = 6.1%	
	Root chloride concentration (%)				
A. albicans	0.48	2.79	3.24	3.19	3.52
ICP 3783	0.81	3.58	2.51	1.30	1.21
A. albicans X ICP 3783	0.73	2.24	3.24	3.54	3.87
ICP 3783 X A. albicans	0.83	2.87	3.46	3.21	3.83
SE ± 0.257		LSD at 5% = 0.76		CV = 14.4%	

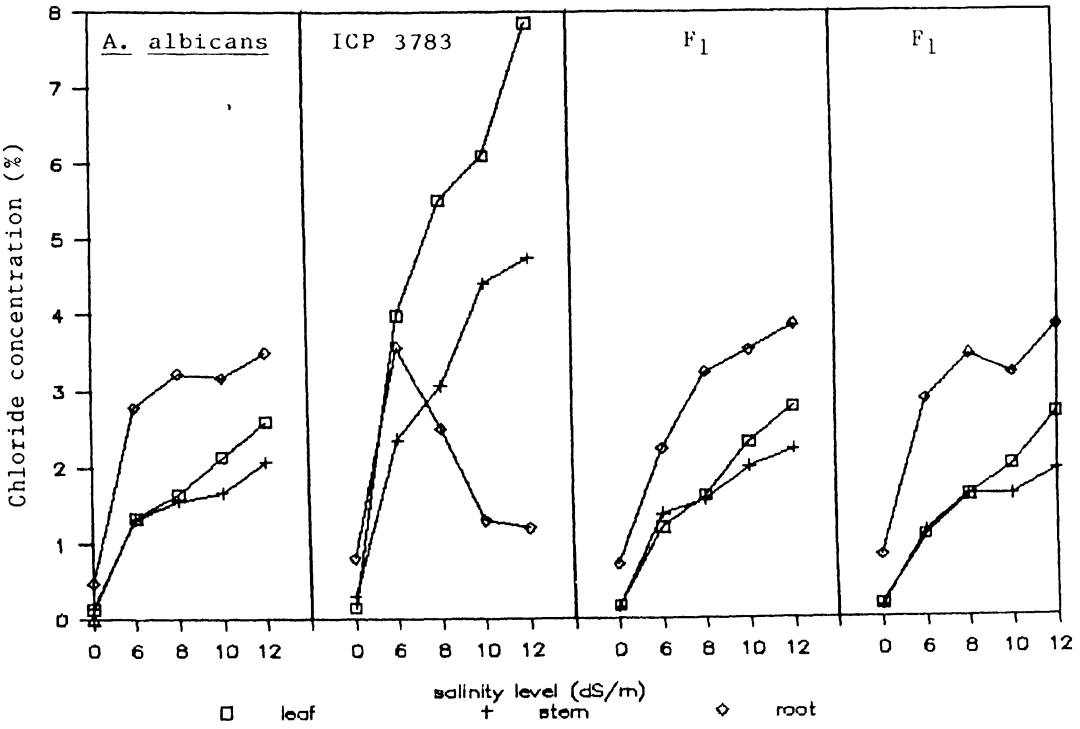

Fig. 4.8.4. Effect of salinity on tissue chloride concentration (%) of A. albicans (tolerant), ICP 3783 (sensitive) and their F_1 hyrbids (A. albicans x ICP 3783 and ICP 3783 x A. albicans).

4.8.4.7 Manganese: Leaf, stem and root manganese levels showed an increase with increasing salinity in all the types (Table 4.8.9). The interaction between salinity level and types in leaf, stem and root manganese levels was significant. The increase in manganese levels in the plant with increase in salinity was highest in ICP 3783 (for stem and root manganese levels, data not presented).

4.8.4.8 Zinc: In A. albicans, there was no significant increase in the zinc levels in the leaf with increasing salinity. The F1 hybrids were almost similar to A. albicans in their zinc content. In ICP 3783, there was a considerable increase in zinc level with salinity.

4.8.4.9 Iron: The iron content of the leaves increased with salinity (Table 4.8.9). ICP 3783 showed the highest leaf iron content of 198 ppm, whereas in A. albicans the iron content in the leaf was as low as 131.6 ppm (average). The leaf iron content in the F1 hybrids was intermediate to their parents.

The results showed that the various charcteristics which might be associated with salinity tolerance were inherited from the parent A. albicans. In this respect there were no reciprocal differences. The salinity tolerance seemed to be under genetic control and found to be a dominant trait.

Table 4.8.9. Response of Atylosia albicans, Cajanus cajan (ICP 3783) and their F1 hybrids to different levels of salinity in relation to leaf, manganese, zinc and iron content (ppm).

Genotypes	Salinity treatment (dS/m) 0	6	8	10	12
			Leaf manganese concentration (ppm)		
A. albicans	71	131	144	144	145
ICP 3783	73	202	294	296	260
A. albicans X ICP 3783	98	119	141	160	148
ICP 3783 X A. albicans	83	140	149	154	171
SE ± 13.49		LSD at 5% = 39.90		CV = 12.2%	
			Leaf zinc concentration (ppm)		
A. albicans	22.5	27.5	22.1	25.1	26.9
ICP 3783	33.2	46.7	41.7	50.3	53.6
A. albicans X ICP 3783	25.2	28.3	38.2	31.5	35.3
ICP 3783 X A. albicans	26.5	39.5	36.2	37.2	31.1
SE ± 2.50		LSD at 5% = 7.39		CV = 10.4%	
			Leaf iron concentration (ppm)		
A. albicans	103	132	133	167	124
ICP 3783	159	202	192	201	239
A. albicans X ICP 3783	172	165	129	195	138
ICP 3783 X A. albicans	133	154	136	180	147
SE ± 15.8		LSD at 5% = 46.7		CV = 14.0%	

5. DISCUSSION

5.1 Genetic variation in pigeonpea germplasm and its wild relatives in response to salinity

Genetic variation in the cultivated species in response to salinity is a prerequisite for improving salinity tolerance of crop species (Shannon, 1985). In pigeonpea, there were significant differences among genotypes in their ability to germinate at 6 dS/m salinity level. Among the 150 accessions tested, the germination was as good as in the control (i.e 100%) in the genotypes ICP 8695, ICP 11878, ICPL 228, ICPL 329. and ICP 8007. Among the 150 accessions tested ICP 8705 showed the maximum reduction (28%) in germination at 6 dS/m. Such genotypic or varietal differences in pigeonpea for germination under saline conditions have also been reported by Paliwal and Maliwal (1973) and Gururajarao et al., (1981). The germination of pigeonpea seems to be relatively tolerant to salinity compared to tolerance at later stages of growth. This is clearly evident at 8 and 9 dS/m salinity levels, where none of the germplasm lines were able to survive even though germination was around 60-80% of the control in most of the accessions.

There was also considerable variation among pigeonpea accessions in survival, shoot dry matter production and leaf necrosis at 6 dS/m. In some accessions (ICP 8594, ICP 8659, ICP 11876) the survival was as good as in the control, whereas there was more than 70% mortality in a number of accessions and in ICP 8663 over 90% mortality was observed. ICPL 227, a breeders promising line, produced the maximum shoot dry matter, equivalent to 71% of its control, without leaf necrosis

symptoms and had 93% survival. In contrast, pigeonpea accessions ICP 11795, ICP 11796, ICP 8663, and HY 3C were the most adversely affected at 6 dS/m, with shoot dry matter reduced to about 15% of the control and plants showing severe necrotic symptoms, and more than 50% mortality. It may be noted that even the most tolerant pigeonpea line, ICPL 227, suffered a growth reduction of nearly 30% at 6 dS/m.

Genetic variation for salinity tolerance has been reported in a number of legumes, namely lentil (Jana, 1979; Rai, 1983), alfalfa (Brown and Hayward, 1956), pea (Cerda et al., 1982), pigeonpea (Gururajarao et al., 1981; Paliwal and Maliwal, 1973; Chauhan, 1987), chickpea (Lauter and Munns, 1986; Saxena, 1987; Goel and Varshney, 1987), subterranean clover (West and Taylor, 1981), cowpea (Paliwal and Maliwal, 1973), soybean (Wieneke and Lauchli, 1979), berseem (Ashraf et al., 1987), and red clover (Ashraf et al., 1987); as well as in some other important crops viz., wheat (Sayed, 1985, Kingsbury and Epstein, 1984;), rice (Ponnamperuma, 1984) and barley (Srivastava and Jana, 1984; Epstein et al., 1980). However, the extent and range of variation within a crop species seems to be relatively limited, probably because most cultivated crop species have been selected in non-saline environments, where salt tolerance traits, if any, would have been gradually lost from their gene pools over hundreds of years of domestication (Mudie, 1974; Maas and Nieman, 1978).

In a few crop species, such as Lactuca sativa (Ayers et al., 1951), Phaseolus vulgaris (Bernstein and Ayers, 1951), Daucus carrota and Allium cepa (Bernstein and Ayers, 1953), little or no variation in salinity tolerance has been detected among cultivars. This is not

surprising since the genetic base of most of these vegetable crop species appears to be very narrow. Also, these crops have long been sheltered from environmental stresses and accumulation of genes favouring good growth in normal soils and water is a logical expectation.

In this study, most of the genetic variation in salinity tolerance for pigeonpea appeared to be confined to a narrow range of salinity levels between 6 to 7 dS/m. There were no substantial differences in growth and survival between the most tolerant pigeonpea genotypes (ICPL 227, ICP 8594, ICP 8659, ICP 10103, and ICPL 112) and the most sensitive ones (HY 3C, ICP 8663, ICP 3783, ICP 9080, and ICP 11772) at 5 dS/m and none of even the most tolerant lines were able to survive at 8 and 9 dS/m. Most of the survival and growth differences between tolerant and sensitive accessions were observed at 6 and 7 dS/m. Keating and Fisher (1985) observed a 50% growth reduction in two pigeonpea varieties within a range of 4.9 to 5.4 dS/m. It is clear that the genetic variation in pigeonpea is confined to a narrow range of salinity, and this may not be sufficient for the genetic improvement of salinity tolerance through selection. It is also to be remembered that field salinity is a dynamic phenomenon where salt concentration may change over time and space, and genotypes selected for saline conditions should be able to perform uniformly across a wide range of salinity levels. To demonstrate genotypic differences under field conditions, these differences between genotypes need to be maintained over a wide range of salinity levels. So unless a wide range of tolerance is identified and made available to breeders, genetic improvement through selection may not be feasible with the

present narrow range of genetic variability.

However, it can not be ignored that there are 10,000 germplasm accessions available in pigeonpea, while in the present study only 150 accessions have been evaluated. The chances of obtaining a wider range of variation to salinity tolerance are still possible. Variations in salt tolerance have been increased through induced mutations (Langridge, 1958; Ashraf et al., 1987;) although such methods have their own limitations (Nilan et al., 1969). There is a growing feeling that the physiological traits that are likely to play an important role in salinity tolerance may have been lost in the cultivated crop gene pools during domestication under very favourable environments (Mudie, 1974; Maas and Nieman, 1978). Wild relatives of the crop species, which have not passed through the rigour of human selection, may provide a better chance of obtaining a source of high level of tolerance to salinity. Introduction of genes from the wild salt tolerant species can be used to enrich the crop species gene pools (Tal, 1985). However, information on the genetic variability for salinity tolerance in wild species, that can be hybridized with crop plants, is very limited. The lack of variation for salinity tolerance in the cultivated tomato (Lycopersicon esculentum) is being overcome by making wide crosses with wild related species (Lycopersicon cheesmani, and Solanum pennellii) which are highly salt tolerant (Tal and Shannon, 1983). Elytrigia elongata, a wild wheat grass is highly tolerant to salinity compared to the cultivated wheat (Triticum aestivum). The tolerance trait was successfully transferred from E. elongata to T. aestivum and was expressed in the amphidiploids (Dvorak and Ross, 1986). Oryza coarctata, a wild rice,

was found to be extremely tolerant to salinity (up to 30 to 40 dS/m), although this species is completely incompatible with the cultivated rice (O. sativa) due to its tetraploid nature and spikelet character (Bal and' Dutt, 1986). Somatic hybridization could provide an opportunity for incorporating the desirable traits of the wild species in to cultivated rice.

Among the wild relatives of pigeonpea tested, various species of Atylosia, Rynchosia, and Dunbaria showed a wide range of variation (4 to 12 dS/m) in their salinity tolerance. A. albicans and A. platycarpa grew and remained healthy even at a salinity level of 12 dS/m. A. platycarpa was able to profusely flower and produced a large number of pods at all salinity levels including 12 dS/m. Rynchosia albiflora proved to be the other extreme, being salt sensitive even at 4 dS/m.

Among the 15 wild types tested, A. platycarpa, A. albicans A. sericea and A. cajanifolia appear to be distinctly superior in their salinity tolerance as compared to even the most tolerant pigeonpea genotype ICPL 227. This certainly raises the possibility of increasing the salinity tolerance of pigeonpea by transferring the higher level of tolerance from these wild types to the cultivated types. A. platycarpa is incompatible for direct hybridization with cultivated pigeonpea and bridging techniques seem necessary to transfer not only salinity tolerance but other desirable traits of this wild species (ICRISAT, 1987). However, A. albicans which has the same level of tolerance as A. platycarpa, is compatible with the cultivated pigeonpea, and the tolerance could thus be transferred to pigeonpea. A. sericea and A. cajanifolia can also act as sources of

tolerance for the genetic improvement of salinity tolerance in pigeonpea as they are also compatible with pigeonpea. The remaining wild types are either at par with the tolerant pigeonpea ICPL 227 or inferior to it, indicating that their role in improving the salinity tolerance in pigeonpea is limited. However, this is based only on one accession from each wild species, and considering the large number of accessions available within each species even higher levels of tolerance than what has been identified in A. albicans and A. platycarpa cannot be ruled out. In any case, the use of wild relatives of pigeonpea could be a major factor in the genetic improvement of salinity tolerance in pigeonpea. It is suggested that there is scope for identifying higher levels of tolerance than the present level and this can be realized through future evaluation of a large number of accessions available among various wild relatives of pigeonpea.

5.2 Physiological basis for the mechanisms of salinity tolerance in pigeonpea and its wild relatives

All of the most tolerant wild types (A. platycarpa, A. albicans, A. sericea and A. cajanifolia) which could survive and grow up to 10 dS/m maintained 5 to 10 times less sodium in leaves and stem compared to the sensitive species, viz., A. acutifolia, A. goensis, A. scarabaeoides and HY 3C. Regulation of sodium, particularly exclusion from the shoot system, appears to be playing an important role in the salinity tolerance in pigeonpea and its wild relatives. Most of the legumes so far studied respond to saline conditions by exclusion of sodium and chloride from the leaves

(Lauchli, 1984). There are several reports of tolerance associated with exclusion of sodium and chloride from the shoot (Greenway, 1965; Abel, 1969; Tiku and Snaydon, 1971; Hannon and Barber, 1972; Downton, 1978; Rozemà et al., 1978; Venables and Wilkins, 1978; Lauchli and Wieneke, 1979; Erdei and Kuiper, 1979; Gorham et al., 1986; Aswathappa and Bachelord, 1986). It has been observed that root sodium levels in the tolerant types increased with increasing salinity to a greater extent than in the sensitive types, which had about 50% less root sodium. This indicates that the sodium retention capacity of tolerant types is more than that of the sensitive types. Atylosia grandifolia and A. reticulata are exceptions to this trend, where root sodium levels were high inspite of these being sensitive types.

This 'efficient sodium regulation capacity' in the tolerant species thus appears to play an important role in the tolerance mechanism. This may involve a series of physiological processes such as, (a) Efficient regulation of sodium influx, (b) high retention capacity of sodium in the root, and (c) sodium reabsorption from the xylem sap through xylem parenchyma transfer cells. Regulation of sodium influx at the membrane level could be possible through efficient K/Na selectivity. Discrimination can be achieved during influx (Rains, 1972) or by K/Na exchange (Jeschke and Nassery, 1981; Jeschke, 1984). High retention capacity of sodium without disturbing the metabolism of root cells can be possible only through sequestration of sodium into the vacuole, i.e., efficient compartmentation, and this could be brought about through an active Na/K exchange operating at the tonoplast. These kinds of sodium pumps are powered by ATP and catalysed by Na-ATPase enzyme, and may have a

central role in salt tolerance (Tal, 1985). There is evidence in barley (Pitman and Saddler, 1967), oat (Pierce and Higinbotham, 1970) and onion (Macklon, 1975) that ionic pumps may be located at the tonoplast, transporting sodium into the vacuole. Existence of sodium and potassium activated ATPases in the roots of Plantago maritima was demonstrated by Kylin and Gee (1970), Kylin (1973), Karlson and Kylin (1974), Nelson and Kuiper (1975), Erdei and Kuiper (1979).

In most of the tolerant wild types (A. albicans, A. sericea, A. platycarpa, and A. cajanifolia) the increase in root sodium levels occurred at 4 dS/m and further increases in root sodium levels with increasing salinity were negligible. There was no major increase in shoot sodium level in any of the salinity levels up to 10 dS/m. This shows that once the sodium compartmentation capacity in the root becomes saturated, these tolerant types are able to regulate the inflow of sodium and that this is coupled with the expansion of compartmentation capacity of the root (due to growth), without translocating it to the shoot. This could be possible if the tolerant wild types possesses sodium pumps at the plasmalemma and at the tonoplast and compartmentation could be effected by selective K influx and Na efflux at the plasmalemma and by Na/K exchange at the tonoplast. The double requirement in salinity tolerance of protecting the cytoplasm against sodium and of maintaining osmotic balance could be met by a combination of an outwardly directed sodium pump at the plamsmalemma and an inwardly directed one at the tonoplast. However, before concluding on possible mechanisms, it would be necessary to conduct more indepth studies on how the sodium is being withheld in the root cells. Studies using X-ray microanalysis and on sodium

efflux are required in the tolerant wild species in order to prove this hypothesis. A similar hypothesis has been proposed by many authors to explain the physiological basis of the mechanisms of tolerance in barley, where root cortex cells are able to sequester predominantly sodium in the vacuole while maintaining a high K/Na ratio in the cytoplasm (Jennings, 1968; Kylin and Hansson, 1971; Jeschke, 1973, 1977, 1979, 1980; Pitman et al., 1981).

High sodium concentrations in the shoot could be prevented if sodium ions are removed from the xylem during upward transport. This occurs in some species, particularly in legumes (Jacoby, 1965; Lauchli, 1976; Yeo et al., 1977; Lauchli and Wieneke, 1979; Walker, 1986), where xylem parenchyma transfer cells play an active role in removing sodium from the xylem sap through active reabsorption by Na/K exchange. There may be a possibility that, in the tolerant wild types, this kind of regulatory mechanism has a role in maintaining low levels of sodium in the shoot. However, this also needs confirmation by further studies on the tolerant wild types.

In the tolerant wild spesies, the tissue potassium levels in leaf, stem and root increased with increasing salinity. In A. albicans, at 10 dS/m salinity level, there was a 65% increase of potassium (%) in the leaf, 106% increase in stem, and a 73% increase in root over control. By contrast, in the sensitive species A. acutifolia, there was a 50% reduction in leaf potassium, 30% reduction in stem and 60% reduction in root potassium levels at 10 dS/m, which indicates the K/Na selectivity was lost in the sensitive types at higher salinity levels.

Efficient regulation of chloride movement into the plant system may also have an important role in the salinity tolerance. In all the tolerant species except A. platycarpa, leaf and stem chloride levels were 2 to 3 times less than in the sensitive species. A. platycarpa is an exception to this trend where leaf chloride levels were high compared to the rest of the tolerant species. This association of tolerance with high leaf chloride levels may be due to an ability to compartmentalise the chloride in the leaf cells without disturbing the metabolism. However, this hypothesis needs confirmation from further studies. It is apparent that root chloride levels of the tolerant species are significantly higher than those of the sensitive species. A. scarabaeoides and A. grandifolia are exceptions to this trend where root chloride levels are as high as in the tolerant types at 10 dS/m, though these species did not survive at this level. It can be concluded that the tolerant wild types are capable of regulating the chloride flow into the system more efficiently compared to the sensitive species. This 'efficient chloride regulation' can involve at least four possible physiological processes. The first is lower influx of chloride at the membrane level through efficient ion selectivity and the second process is high chloride retention ability in the root cells through effective compartmentation in the vacuoles, which requires specific ionic pumps (chloride pumps) operating at the tonoplast powered by ATP and catalysed by Cl-ATPase. Existence of Cl stimulated ATPase has been reported by Hill and Hill (1973). Thirdly, chloride regulation is also possible through activation of chloride efflux pumps at the plasmalemma of roots, once the chloride retaining capacity of the root is saturated. Existence of chloride efflux pumps at the plasmalemma of Avena sativa has been reported by Pierce and

Higinbotham (1970). For salinity tolerance, the requirement of protecting the cytoplasm against chloride, and of maintaining osmotic balance by accumulating chloride in the vacuole could be met by a combination of an outwardly directed Cl pump at the plasmalemma and an inwardly directed one at the tonoplast. It is seen that in the tolerant species, the root chloride levels did not increase very much at 6 dS/m and above, and has been effectively regulated in the shoot. This shows that these tolerant types are able to regulate the chloride flow into the shoot system through some mechanism once the chloride retention capacity is saturated. The fourth process could be the retranslocation of chloride from the shoot to the root via phloem. Such retranslocation of chloride from shoot to root through the phloem has been reported by Winter (1982). These different physiological processes involved in the efficient chloride regulation need complete co-ordination at the whole plant level, and failure at any level would lead to a breakdown of the entire chloride regulatory system, resulting in chloride toxicity and death of the plant.

It is seen that the level of magnesium in the leaf has remained unaffected with increasing salinity in the tolerant species, while there was more than 50% reduction in the sensitive species. The increase in the uptake of micronutrients (Mn, Zn, Fe) with increasing salinity in all cases indicates that micronutrient availability during saline conditions may not be the limiting factor for growth.

Various organic solutes increase under high salinity conditions in many species (Gauch and Eaton, 1942; Bernstein and Ayers, 1953; Storey and Wyn Jones, 1977) and can contribute to osmotic balance (Stewart and Lee, 1974) or enzyme protection (Pollard and Wyn

Jones, 1979), or perform other protective roles (Greenway and Munns, 1980; Gorham et al., 1985). In the present experiment, an increase in leaf proline with increasing salinity was noticed in some of the wild species of pigeonpea including Atylosia lineata, A. sericea, and A. lanceolata. However, in most other species and genotypes there was no accumulation of proline. A wide range of organic solutes such as sucrose, sorbitol, mannitol, pinitol, glycinebetaine, B-alaninebetaine, prolinebetaine, 3-dimethyl sulfonio-propionate can perform similar protective roles during saline conditions (Greenway and Munns, 1980; Gorham et al., 1985). Since only the proline accumulation was measured in these studies it can atleast be said that this compound is not directly related with salinity tolerance.

While dealing with the mechanism of salinity tolerance it can be concluded that tolerance is a product of many physiological processes and no single factor alone can be responsible for tolerance to salinity. It is a co-ordination at the whole plant level among various physiological processes involved that contribute to higher levels of salinity tolerance. The survival value or positive role of any physiological trait in salinity tolerance depends on the presence of other physiological traits. For example, efficient sodium regulation capacity can play its role in salinity tolerance only if the species also has efficient potassium selectivity and/or efficient chloride regulation capacity. Similarly, within a physiological trait, for example, in 'efficient sodium regulation' a series of physiological processes are involved in the proper functioning of this trait in maintaining the lower sodium levels in the shoot. Since functioning of each physiological process involved in salinity

tolerance depends on the functioning of the other physiological processes, a breakdown at any level could lead to the collapse of the whole regulation system.

5.3 Role of calcium in salinity tolerance

It has been observed that growth was better in both tolerant (ICPL 227) and sensitive (HY 3C) genotypes with increasing calcium level in the medium at 6 and 8 dS/m salinity treatments. This positive growth response to increasing calcium level under salinity (NaCl) conditions is in agreement with the previous studies in barley (Hyder and Greenway, 1965), Phaseolus vulgaris (Lahaye and Epstein, 1971), and in wimmera rye grass (Marcar, 1986). Although growth is improved in tolerant as well as sensitive genotypes with increasing calcium levels during salinity, the relative growth differences between tolerant and sensitive genotypes were maintained at all the calcium levels within salinity treatments.

The response of different species to high Na/Ca is related to differences in their membrane structure, a concept proposed by Greenway and Munns (1980). This is based on the studies of Bower and Wadleigh (1948) and Eaton (1942) who reported that species which are most sensitive to high Na/Ca per se were also most sensitive to high concentrations of soluble salts; for example, beans are extremely sensitive and sugarbeet is very tolerant to both conditions. The persistence of relative growth differences between tolerant and sensitive genotypes with increasing calcium levels in the medium may be due to differences in their membrane structure.

In pigeonpea, at 0.36mM calcium level in the medium, the tissue calcium levels decreased at 6 and 8 dS/m salinity treatments in both tolerant and sensitive genotypes, although the sensitive genotype suffered greater reduction compared to the tolerant genotype. The presence of potentially toxic ions (particularly sodium) will increase the possibility of membrane damage. Under low calcium levels (<1mM) NaCl salinity reduces the calcium uptake and translocation (Gerard and Hinojosa, 1973; Lynch and Lauchli, 1985), and this could reduce the membrane associated calcium due to displacement of calcium by sodium, thus disrupting the membrane integrity (Cramer et al., 1987). In studies with Agropyron elongatum (tolerant) and A. intermedium (sensitive), Elzam and Epstein (1969) found that tolerant species which could grow well at 50 mM NaCl salinity was able to maintain calcium uptake when compared to sensitive species which could not maintain calcium uptake.

At 0.36 mM calcium level, the sodium levels in the tissue was very high in both the genotypes and decreased with increasing calcium level at 6 and 8 dS/m treatments. The higher amount of sodium in tissue (leaf, stem and root) can be attributed to membrane damage caused by a decrease in tissue calcium level. In Phaseolus vulgaris, low calcium per se could increase the membrane permeability to sodium (Lahaye and Epstein, 1971). It is likely that a decrease in membrane associated calcium content through displacement of calcium by sodium disrupts the membrane integrity (Cramer et al., 1987). The decrease in the tissue sodium levels with increasing calcium level in the medium in pigeonpea genotypes could be due to improvement of tissue calcium status leading to the maintenance of membrane integrity

preventing passive movement of sodium and enhancement of the selective ion uptake property or prevention of the uptake and translocation of sodium into the plant by competitive effects. The tolerant genotype (ICPL 227) maintained lower tissue (leaf, stem and root) sodium levels at various calcium levels in the medium compared to the sensitive genotype at 6 and 8 dS/m salinity levels, suggesting that different genotypes may respond differently to external calcium levels during salinity. This may be due to differences in their membrane structure, but this hypothesis needs direct support from studies on membrane structure, which is not yet available, for any legume.

Interestingly, an increase in potassium levels in leaf, stem and root with increasing calcium concentration in the medium at 6 and 8 dS/m salinity treatments has been noticed. This type of enhancement of potassium uptake is in agreement with the earlier reports. Cramer et al. (1985) showed that calcium could play an important role in minimizing the leakage of cytoplasmic potassium. Calcium is also known to enhance the selective absorption of potassium (Rains and Epstein, 1967; Elzam and Epstein, 1969; Kent and Lauchli, 1985). Modification of selectivity of the cell membrane for monovalent cations could be influenced by the external calcium levels (Jacobson et al., 1960; Moore, 1960). Due to improvement of potassium uptake and reduced sodium uptake in pigeonpea, the potassium/sodium ratio in the plant increased with increasing calcium level at 6 and 8 dS/m salinity treatments. In the tolerant genotype, higher K/Na ratio was maintained at all calcium levels under salinity compared to sensitive genotype.

Increasing calcium in the medium during salinity, also increased the chloride concentration in both tolerant and sensitive genotypes, although the increase was significantly higher in the sensitive than in the tolerant genotype. This study reports for the first time that calcium can enhance chloride uptake under saline conditions. However, calcium can enhance the uptake of several anions, such as NO3, Br, Cl, and SO4, under non-saline conditions (Hooymans, 1964). In a recent study with cotton, Ward et al. (1986) showed that calcium in the medium could enhance the NO3 uptake during NaCl salinity. The reasons for enhancement of chloride uptake are not clear and it is suspected that this enhancement may negate positive effects of enhanced K/Na selectivity under saline conditions.

In conclusion, it can be stated that the positive growth response in pigeonpea genotypes with increasing calcium during saline conditions could be due to: (a) maintenance of membrane integrity preventing passive movement of sodium, (b) retention of membrane selective permeability leading to enhancement of K uptake and increase in the K/Na ratio in the cytoplasm, essential for normal metabolism. It is intriguing that the relative growth differences between tolerant and sensitive genotypes persisted across various calcium levels at 6 and 8 dS/m salinity treatments. This has practical importance since field salinity is a complex problem and the relative concentrations of sodium and calcium may vary from place to place. Genotypes selected for saline conditions should be able to perform uniformly across the various sodium/calcium levels.

5.4 Response of the pigeonpea-*Rhizobium* symbiosis to salinity stress

Significant differences in pigeonpea growth were noticed among plants inoculated with different rhizobia and grown at different salinity levels indicating the existence of variation among rhizobial strains in their nitrogen-fixing ability under saline conditions. These differences were most conspicuous at 8 dS/m salinity level. Plants treated with IC 3024, IC 3484, IC 3195 were more affected by salinity at 6 and 8 dS/m compared to IC 3087 and IC 3506, indicating that the former group of rhizobial strains were more sensitive to salinity. This confirms the existence of rhizobial variation in symbiotic ability under saline conditions, which is a basic prerequisite for any selection of rhizobial strains for saline soils. In rhizobial treatments IC 3087 and IC 3506, the growth was equally good as in the N-fed treatments at 4 and 6 dS/m. However, at 8 dS/m, the N-fed treatment showed better plant growth compared to any of the rhizobial treatments, indicating that even the best rhizobial strains (IC 3087 and IC 3506) could not support adequate plant growth at 8 dS/m salinity level. In the wild species *Atylosia platycarpa*, there was no significant difference in growth between N-fed and plants inoculated with IC 3087 up to 10 dS/m, suggesting that the symbiotic ability of IC 3087 was adequate to support growth. This demonstrates that symbiotic sensitivity to salinity varies between hosts and the rhizobium strains.

Salt resistance of legumes may vary with the mode of nitrogen acquisition. Growth of soybean (Bernstein and Ogatta, 1966), *Glycine wightii* (Wilson, 1970), chickpea (Lauter et al., 1981), and *Vicia faba* (Yousef and Sprent, 1983) were more affected by salinity when grown

symbiotically than under nitrogen fertilization, whereas, in alfalfa, relative inhibition of growth by salinity was similar for nitrogen fertilized and nitrogen fixing plants (Bernstein and Ogatta, 1966). Rhizobial strains of single species can also vary in their symbiotic ability under saline conditions (Rai, 1983).

Nodule initiation in the legume-Rhizobium symbiosis involves a complex interaction between host root, rhizobial strain and the environment. Salinity may differentially affect each phase of the legume-Rhizobium symbiosis: viz., rhizobial survival and growth in the rhizosphere of the host, rhizobial infection of host root hair, nodule initiation and development, nodule functioning (nitrogen fixation), and growth of the host legume.

In general, Rhizobium strains can grow and survive at salt concentrations which are inhibitory to most agricultural legumes (Singleton et al., 1982). From previous studies on salinity tolerance of pigeonpea rhizobia (Subbarao et al. unpuplished data) revealed that many rhizobia could grow easily at NaCl concentrations that are inhibitory to the host plant, and survival and multiplication of Rhizobia may not be the limiting factor for establishing a symbiosis under saline conditions. This is in agreement with the findings of others - Glycine max (Singleton and Bohlool, 1984), Pisum sativum (Siddique et al., 1985) and Medicago sativa (Lakshmi Kumari et al., 1974).

In the early inoculated (IC 3024) treatment of pigeonpea, nodulation seemed to be little affected at 6 and at 8 dS/m salinity levels, whereas in the late inoculated treatment, nodulation has been

totally suppressed at 8 dS/m, indicating that IC 3024 was sensitive to salinity during early stages of nodule formation. In Atylosia platycarpa,, for the late inoculated IC 3087 rhizobial treatment, nodule number increased with increasing salinity up to 10 dS/m salinity level, without being affected at 12 dS/m, suggesting that sensitivity of the nodulation process to salinity depends on Rhizobium strain. With A. platycarpa, for the early inoculated treatment, the nodule number decreased at 8 dS/m and above but the reasons for this are not known.

There are differences among rhizobial treatments with IC 3024, IC 3484, IC 3087, IC 3506 and IC 3195 in nodulation during salinity. In all the rhizobial strains, nodule number decreased with increasing salinity, except in IC 3087 where nodule number in pigeonpea increased with salinity up to 8 dS/m. This shows the existence of variation in the ability of rhizobial strains to nodulate during salinity stress. This is in contrast to the general reduction in nodule number with increasing salinity in Glycine max (Singleton and Bohlool, 1984), Pisum sativum (Siddiqui et al., 1985) and Vicia faba (Yousef and Sprent, 1983). In Glycine max, even 2.7 dS/m could suppress 50% of the nodulation with nearly total suppression at 8.0 dS/m, a response similar to that observed for IC 3024 in this study. The observation that nodule number increased with salinity is probably the first report.

In all the rhizobial treatments, no significant change in the average nodule dry weight with salinity treatment has been noticed, except in IC 3195 where it increased with salinity. In IC 3087, the average nodule weight appeared to be reduced to 50% of the control,

however, this was not statistically significant due to the very low average nodule dry weight compared to the other rhizobial treatments. Nodule development was not affected with increasing salinity in soybean (Singleton and Bohlool, 1984); while in Vicia faba, nodule size increased with salinity, probably to compensate to a certain extent the reduced nodule number (Yousef and Sprent, 1983). Total nodule dry weight has decreased with increasing salinity in all the rhizobial treatments and this could be merely a consequence of the reduction in the number of nodules, except in in IC 3087 where it was due to the reduction in the average nodule weight.

Total nitrogenase activity decreased with increasing salinity in all the rhizobial strains. This can be a consequence of the reduction in the nodule number and total nodule dry weight since specific nitrogenase activity in several rhizobial treatments has remained unaffected with increasing salinity. In rhizobial treatment with IC 3195, the specific nitrogenase activity increased at 8 dS/m, which can be attributed to the severe reduction of nodule number and nodule dry weight. The results suggest that the functioning of nodules was not affected by increasing salinity in cultivated pigeonpea. In Atylosia platycarpa, specific nitrogenase activity, however, exhibited a decrease with increasing salinity. This indicates that nodule functioning during salinity may vary with the host and depends on the extent of effect on nodulation and the ability of the host to support the energy requirements of the Rhizobium. In soybean (Singleton and Bohlool, 1984), Macroptilium atropurpureum and Neotonia wightii (Wilson, 1985), specific nitrogenase activity was not affected by salinity, whereas in Vicia faba (Yousef and Sprent, 1983) specific

nitrogenase activity decreased with increasing salinity.

The nitrogen levels in the leaves of the N-fed treatment increased with salinity. In rhizobial treatment, IC 3087 and IC 3506, there was no significant change in the leaf nitrogen, whereas in rhizobial treatments IC 3024, IC 3484 and IC 3195 leaf nitrogen levels decreased with salinity. This confirms that rhizobial treatments which suffered severe reduction in nodulation at 6 and particularly at 8 dS/m salinity levels were not able to meet the nitrogen requirements of the host and thereby leading to internal nitrogen deficiency. In A. platycarpa, leaf nitrogen levels increased in the N-fed treatment and decreased in the inoculated treatment with increasing salinity, although nitrogen levels in pod, stem and root increased in both N-fed and inoculated treatments. It may be noted that in this wild species, plants were close to maturity at the time of harvesting and this could be one of the reasons for the decrease in the leaf nitrogen levels in the inoculated treatments. In Vicia faba, in N-fed treatment leaf nitrogen level increased with salinity, whereas in Rhizobium-inoculated treatments nitrogen levels decreased (Yousef and Sprent, 1983). The present results are broadly in agreement with this although in a few strains leaf nitrogen levels remained unaffected by salinity treatment.

Leaf phosphorus levels were increased with salinity in all the rhizobial treatments as well as the N-fed treatment. This suggests that phosphorus uptake would not be a limitation for nitrogen fixation under saline conditions. Wilson (1970) reported that in soybean, phosphorus levels in leaf and stem decreased at high salinity (15 dS/m) in the rhizobial treatments and remained uneffected in the

It can be concluded that in pigeonpea, there is variation in the symbiotic ability of rhizobia during salinity stress, which indicates some scope for improvement of nitrogen fixation of pigeonpea in saline soil through the selection of rhizobia. If an appropriate rhizobial strain is found, the pigeonpea-Rhizobium symbiotic system may be able to fix enough nitrogen for the requirements of the host under saline conditions. Although one of the most efficient rhizobium strains, IC 3087, was collected from a saline soil, the other equally efficient strain IC 3506 was collected from a non-saline soil, which shows that selection of rhizobial strains for saline soils need not necessarily be confined to the strains derived from saline soil. This is in agreement with the views of Bharadwaj (1975).

5.5 Inheritance of salinity tolerance

When the salinity tolerance of Atylosia albicans, Cajanus cajan genotype ICP 3783 and their F1 hybrids from reciprocal crosses were tested it was found that A. albicans had a higher level of tolerance to salinity and could grow without salt damage symptoms even at 12 dS/m, compared to the pigeonpea genotype ICP 3783 which suffered a severe growth reduction even at 8 dS/m and failed to survive at 10 and 12 dS/m salinity levels. The F1 hybrids showed an equally high level of tolerance to that of A. albicans, suggesting that the tolerance trait is due to a dominant gene or genes. Absence of differences in plant growth at any of the salinity levels between F1 hybrids shows the absence of a cytoplasmic factor involvement in this trait.

In studies with ecotypes of Festuca rubra, it was shown that salinity tolerance can be a dominant genetic factor (Venables and Wilking, 1978). In Oryza sativa, Akbar and Yabuno (1975) observed expression of the tolerance trait in the F1 hybrids, from a cross of Jhona 349 (tolerant) X Magnolia (sensitive) varieties. In soybean, tolerance was found to be a dominant genetic factor (Abel, 1969). In studies with wild relatives of tomato (Tal and Shannon, 1983), it was found that the salinity tolerance trait from wild type Solanum pennellii expressed as a dominant character in the F1 hybrids of Lycopersicon esculentum X Solanum pennellii. From an inter-generic hybrid, Triticum aestivum (salt sensitive) X Elytrigia elongata (salt tolerant), it was concluded (Dvorak and Ross, 1986) that the tolerance trait was found to be expressed in the amphidiploids. Our results indicating the mode of inheritance of salt tolerance trait from a wild type (A. albicans) in the F1 hybrids of A. albicans X ICP 3783, is in general agreement with the above reports. The genetic determination of salinity tolerance can only be completely understood after studying the inheritance pattern in the F2 and subsequent generations, to be taken up in future.

Tolerances to salt, or other stresses are considered 'complex' characteristics (Ramage, 1980; Woolhouse, 1981) and much of this complexity stems from lack of co-ordinated physiological genetic research (Tal, 1985). It is felt that to resolve such complex problems, the genetic and plant physiology approaches must merge towards a more comprehensive approach to breeding for environmental stress resistance (Blum, 1988). The basic interest should be to identify the precise physiological events under genetic control.

The present studies have shown that the tolerant wild type A. albicans, is efficient in regulating sodium movement by retaining large quantities in the root and allowing a negligible amount into the shoot. This is in contrast to the physiological processes in the sensitive pigeonpea genotype, ICP 3783, where large quantities of sodium accumulate in the shoot and it was unable to retain high amounts of sodium in the root at 8 dS/m and above. It is possible that low potassium levels in the root of the sensitive genotype at 10 and 12 dS/m could be responsible for the decline in the sodium retention capacity of the root, since potassium is apparently required for the retention of sodium in the roots (Besford, 1978).

This 'efficient sodium regulation capacity' in A. albicans is a trait where a series of physiological processes may be involved including: (a) efficient regulation of sodium influx at the membrane level, (b) high retention capacity of sodium in root, (c) removal of sodium from the xylem sap through the active reabsorption through xylem parenchyma transfer cells and (d) retranslocation of sodium from shoot to root, as discussed earlier (section 5.2). Root magnesium levels have also been observed to be lower in the sensitive genotype, ICP 3783, at 10 and 12 dS/m compared to the wild tolerant type, A. albicans, although the differences were not statistically significant. However, one cannot overlook the possibility that the reduced magnesium levels in roots could effect the Na and K activiated ATPases which in turn could effect the sodium retention capacity of the root, since most of the Na and K stimulated ATPases require magnesium for maximal activity (Karlson and Kylin, 1974). The extent of this factor in determining the inability to retain high levels of sodium in the

root of the senstive type at higher salinity (at 8 dS/m and above) levels needs to be determined.

Lauchli (1984) proposed a model to explain the various steps involved in the efficient sodium regulation in a glycophyte. The various physiological processes that have been proposed for the efficient sodium regulation in the tolerant wild type are probably similar to this model (Fig 5.5.1). The various physiological processes involved in the 'effective sodium regulation' have to be co-ordinated and are likely to be controlled by several genes. In our studies with pigeonpea, it is evident that the 'efficient sodium regulation capacity' from the A. albicans was expressed in the F1 hybrids and was under genetic control. In Oryza sativa, it has been observed that efficient sodium regulation was under the control of 3 groups of genes (Akbar et al., 1986). In Aegilops squarrosa it was found that the 'D' genome was responsible for efficient K/Na selectivity which confers higher salinity tolerance when compared to Triticum aestivum (Shah et al., 1987). The wild type was also able to maintain higher levels of potassium at all the salinity levels up to 12 dS/m in various plant parts, viz., leaf, stem and root. In the sensitive genotype ICP 3783, potassium level in various plant parts declined at 8 dS/m or higher salinity levels. In the F1 hybrid, a high level of potassium in the plant indicates that this efficient K/Na selectivity is a heritable trait. It is not known whether the same gene or genes which regulate the sodium flow into and compartmentation with the root cells are also responsible for greater potassium selectivity. However, it is likely that regulation of sodium and higher potassium uptake are inter-related, ie. if a

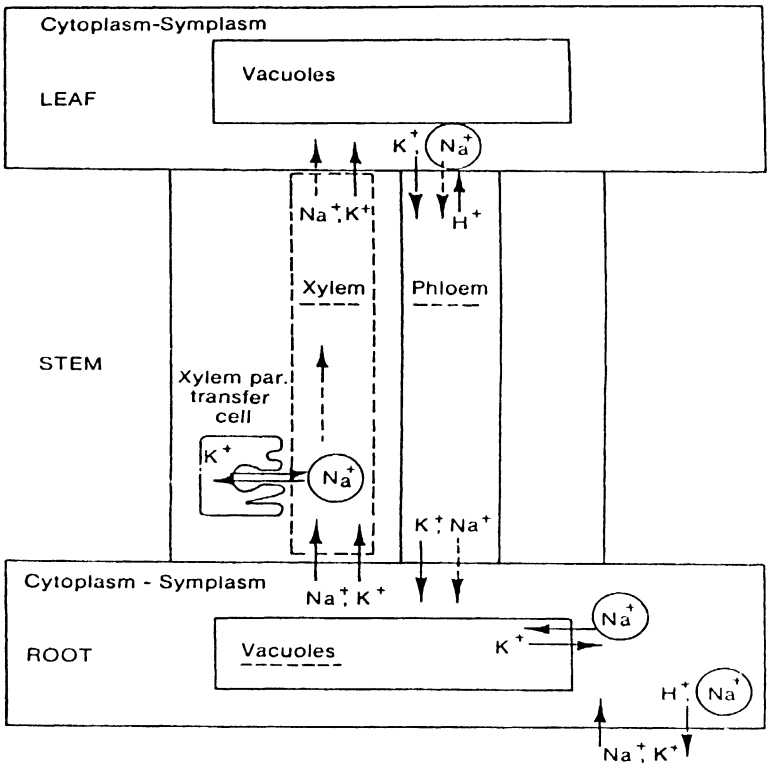

Fig. 5.5.1 **Model of the regulation of Na transport in a Na-excluding glycophyte (Lauchli 1984).**

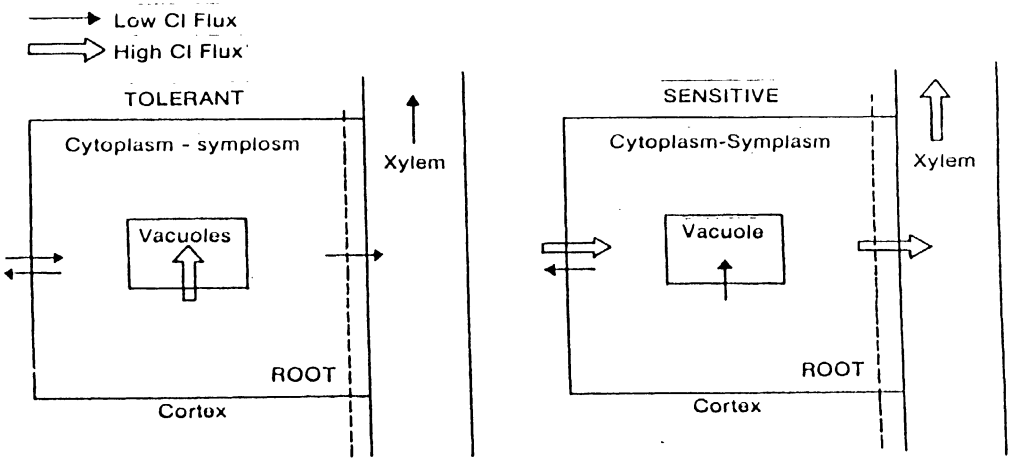

Fig. 5.5.2 **Model of the regulation of Cl transport in roots of salt tolerant and sensitive glycophytes (Lauchli 1984).**

genotype is able to prevent sodium uptake it could permit potassium into the plant system for maintaining electrical balance. It does not exclude the possibility that efficient potassium uptake is controlled by a gene/genes, which is activated if the genotype efficiently regulates the sodium influx and compartmentation. In Lycopersicon pennellii, low level of potassium, which characterizes this wild species, is dominant over high potassium level exhibited in L. esculentum and the number of genes controlling this is low (Tal and Shannon, 1983).

The sensitive genotype, ICP 3783 suffered a severe reduction in transpiration at various salinity treatments. This in turn should affect the photosynthesis and growth of the plant. By contrast, the tolerant wild type was able to maintain the normal transpiration rate even up to 12 dS/m. The F1 hybrids also showed normal transpiration at all the salinity levels, including 12 dS/m. It is not known whether severe reduction in the transpiration rate observed at 8 dS/m or high salinity levels in the sensitive pigeonpea genotype is due to the root's inability to meet transpiration requirements. This can also result from the inability to maintain influx of potassium to the guard cells of the stomata for turgor maintenance which may be related to decreased potassium uptake and high sodium levels under conditions of high salinity. This is expected because potassium plays a major role as an inorganic solute in maintaining the turgor of the guard cells (Humble and Hsiao, 1969; Hsiao, 1976). Further studies are required to determine which alternative is responsible for the severe reduction in the transpiration rate at high levels of salinity in the sensitive type. In Phaseolus vulgaris, stomatal conductance was

reported to have declined with increasing salinity (Seemann and Critchley, 1985). In citrus leaves high concentrations of sodium reduced the transpiration rate and photosynthesis (Behboudian et al., 1986). From the studies in wild tomato (Lycopersicon peruvianum), it has been suggested (Tal and Gavish, 1973; Gertel and Tal, 1986) that the lower stomatal conductance of wild types at high salinity levels was responsible for higher water use efficiency, which could be one of the attributes for its higher level of tolerance to salinity. However, the present results do not support this hypothesis. The tolerant wild type (Atylosia albicans) has been able to maintain higher transpiration rates either because of the ability of the root system to meet the demands of transpiration during salinity stress, or because stomatal opening is maintained due to higher potassium uptake ability.

The tolerant A. albicans was capable of regulating the chloride movement into the plant system by effectively retaining the chloride in the root, which allows relatively less translocation of chloride to the shoot. By contrast, the sensitive pigeonpea genotype ICP 3783, permits large quantities of chloride to move into the shoot system without being able to retain this in roots at higher salinity levels. The efficient chloride regulation capacity in A. albicans is a trait where a series of physiological processes may be involved including: (a) lower influx at the membrane level, (b) high chloride retention capacity of the root system through effective compartmentation, (c) retranslocation of chloride from the shoot to root through phloem. The various physiological processes that are likely to be responsible for the efficient regulation of chloride in the plant system are

similar to the model proposed by Lauchli (1984) (Fig. 5.5.2) to explain the differences in two soybean cultivars in salinity tolerance and their chloride uptake behaviour. The response of F1 hybrids in the chloride regulation behaviour at various salinity levels is similar to that of the tolerant wild type. In soybean, it has been reported (Abel, 1969) that the translocation of chloride from root to shoot is controlled by a pair of genes, where the 'NCl' gene is a dominant factor which effectively excludes chloride from the shoot and has been termed as 'excluder'; and the recessive gene 'ncl' permits large chloride quantities into the shoot and has been termed as 'includer'. Wieneke and Lauchli (1979) have shown that chloride influx into roots of tolerant soybean variety 'Lee' has been much lower than in the salt sensitive non-excluding variety 'Jackson'. It is also suggested (Lauchli and Wieneke, 1979) that in 'Lee' chloride accumulation in the root is mediated by sequestration of chloride into the vacuoles of the cortical cells.

The increased uptake of micronutrients (Mn, Zn, and Fe) observed in various plant parts in A. albicans, ICP 3783 and the F1 hybrids was similar, indicating that the uptake of these micronutrients is not a limiting factor for growth under saline conditions. A high concentration of some micronutrients in the sensitive genotype ICP 3783, in comparison with the tolerant wild type, is possibly a mere consequence of retarded growth.

The results clearly demonstrate the various physiological processes that are responsible for the greater tolerance of the wild type, in comparison with the sensitive pigeonpea genotype, are under genetic control. The expression of physiological traits such as

efficient sodium and chloride regulation capacity, high potassium absorption capacity, and maintenance of stomatal conductance during saline conditions in the F1 hybrids clearly shows that these physiological traits are heritable and are dominant in nature. A dominant gene with pleiotropic effects can be one explanation. However, all these physiological processes need to operate in a very co-ordinated manner, and it is equally possible that these are under the control of a number of genes, most probably closely linked and inherited as one unit. Such a possibility receives support from the concept of Shannon (1985) that 'salinity tolerance is probably the expression of a number of genes and the importance of each is dependent upon its interaction with other salinity tolerance genes and the external salt concentrations'. From the present study it is only clear that the high level of salinity tolerance discovered in the wild type of pigeonpea Atylosia albicans has sound physiological basis. Expression of these physiological traits in the F1 hybrids involving the wild type A. albicans and the cultivated pigeonpea genotype ICP 3783 clearly demonstrate that these traits are inherited and are dominant in nature. Detailed studies on the segregation pattern in the F2 and F3 generations, and analysis of the physiological behaviour can, in future, establish the genetic basis of the physiological traits observed in the wild type of pigeonpea.

6. SUMMARY

Salinity of soil or water presents a stress condition for crop plants that is of increasing importance in agriculture. Development of salt tolerant crops provides an additional option for growers in arid and semi-arid regions to cope with the salinity problems. Pigeonpea (Cajanus cajan)is a major pulse crop of semi-arid regions where salinity problems tend to be acute. The present investigation was undertaken with the objectives of: a) assessing the exploitable genetic variation for salinity tolerance in pigeonpea and its wild relatives, b) understanding the physiological and genetic basis of the traits that confer salinity tolerance, and c) studying the response of the pigeonpea-Rhizobium symbiotic system in saline environments.

A hydroponic screening technique was developed which permitted reliable evaluation of a large number of pigeonpea germplasm accessions for salinity tolerance. It was observed that in pigeonpea germination was less sensitive to salinity compared to later stages of growth. There was considerable variation among the pigeonpea genotypes in their ability to grow in a saline environment. At 6 dS/m salinity level, a breeders' promising line 'ICPL 227' was identified as the most tolerant among 150 lines, and 'HY 3C' was found to be the most sensitive genotype. It was noticed from the growth and survival that most of the genetic variation in pigeonpea was confined to a narrow range of salinity, i.e., between 6 and 7 dS/m. There were no substantial differences between the tolerant and sensitive lines at 5 dS/m and none of the lines were able to survive at 8 dS/m.

Among the wild relatives of pigeonpea, various species of Atylosia, Rynchosia and Dunbaria showed a wide range of variation in their salinity tolerance. Atylosia albicans and A. platycarpa were found to tolerate and grow at a salinity level as high as 12 dS/m. Rynchosia albiflora proved to be the most sensitive wild species and could not tolerate salinity above 4 dS/m.

In pigeonpea and its wild relatives, tolerance to salinity was found to be associated with: a) regulation of sodium and chloride movement into the plant, particularly exclusion from the shoot system, b) high sodium and chloride retention capacity of the root system, and c) high potassium/sodium selectivity. The sensitive species had 5 to 10 times more sodium and 2 to 3 times more chloride in the shoot system and half as much of these ions in the root system, compared to tolerant species. The tolerant species also maintained higher selectivity of potassium/sodium at all the salinity levels up to 12 dS/m, whereas in the sensitive species this selectivity was lost at 8 dS/m and higher salinity levels.

The level of magnesium in the leaves of tolerant types remained unaffected with increasing salinity while in the sensitive species there was about a 50% reduction in the leaf magnesium level. Concentrations of the micronutrients Mn, Zn and Fe increased with salinity in all the species, irrespective of their tolerance to salinity, indicating that micronutrient availability was not a limiting factor for growth under saline conditions. No relationship was observed between proline accumulation in the leaves and salinity tolerance in the cultivated or wild pigeonpea.

There was a positive growth response of the pigeonpea genotypes ICPL 227 and HY 3C to increasing calcium level in the medium undr saline conditions. This response was greater in the tolerant type (ICPL 227) compared to the sensitive type (HY 3C). The relative growth differences between tolerant and sensitive genotype persisted irrespective of the relative sodium and calcium levels in the medium at 6 dS/m and 8 dS/m salinity levels. Under saline conditions, an increase in the calcium level in the medium improved the uptake of potassium and reduced the sodium uptake, and thus the K/Na ratio in the plant was increased. Chloride uptake was also enhanced with an increase in the calcium level and such enhancement was observed to be more in the sensitive genotype.

Significant variation was observed among pigeonpea rhizobia as to their symbiotic ability under saline conditions. Pigeonpea plants inoculated with rhizobial strains IC 3087 and IC 3506 were less affected at 6 or 8 dS/m salinity level than plants inoculated with IC 3024, IC 3484 and IC 3195 strains. In the plants inoculated with IC 3087 and IC 3506, the growth was as good as the nitrogen-fed treatments at 6 dS/m. Only at 8 dS/m did the nitrogen-fed plants suffer less reduction in growth compared to any of the rhizobial treatments. In Atylosia platycarpa, there was no significant difference in growth between the nitrogen-fed and rhizobial (IC 3087) inoculated treatments even at 10 dS/m salinity level. The sensitivity of the symbiotic process to salinity varied between host genotype and between rhizobial strains.

In IC 3087 inoculated plants, the nodule number increased with salinity, although the nodule number of plants inoculated with other rhizobial strains generally decreased with increasing salinity. The average nodule dry weight and the specific nitrogenase activity of the nodulated roots in all the rhizobial strains remained unaffected with increasing salinity. The leaf phosphorus levels increased with salinity in both the nitrogen-fed and rhizobial inoculated plants. There were no major differences between nitrogen-fed and rhizobial treatments in leaf sodium and chloride levels at various salinity levels.

The results clearly demonstrated the potentiality of transferring a trait like salinity tolerance to the cultivated pigeonpea from its wild relatives. The high level of salinity tolerance exhibited by the wild type Atylosia albicans was heritable as a dominant trait as the F1 hybrids of A. albicans (tolerant) X Cajanus cajan ICP 3783 (sensitive) showed comparable levels of salinity tolerance. The absence of differences between the reciprocal crosses indicated that there was no maternal or cytoplasmic factors involved in this trait.

It was established that the physiological traits conferring salt tolerance namely, efficient sodium and chloride regulation capacity and particularly exclusion of these ions from the shoot system while being able to retain an excess of these ions in the roots, are under genetic control. This is a dominant trait and could be transferred to cultivated pigeonpea so as to substantially enhance its salinity tolerance. There is also scope for improvement of nitrogen fixation of pigeonpea in saline soil through selection of rhizobial strains better able to form effective symbiosis under saline conditions.

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Salinity tolerance in pigeonpea (Cajanus cajan (L.) Millsp) and its wild relatives

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ABSTRACT

In pigeonpea genetic variation for salinity tolerance appeared to be confined to a narrow range of salinity levels (6 to 7 dS/m). In wild relatives of pigeonpea (Atylosia, Rynchosia and Dunbaria sp), there is a wider range of variation (4 to 12 dS/m) in salinity tolerance. A. albicans and Atylosia platycarpa were the two most tolerant wild types that could grow up to 12 dS/m. Salinity tolerance seems to be associated with exclusion of sodium and chloride from the shoot system, high potassium/sodium selectivity and high retention of sodium and chloride in the root system. These physiological traits, which are believed to be responsible for the higher level of tolerance to salinity in A. albicans, were uniformly expressed in the F1 hybrids (reciprocal crosses) of A. albicans (tolerant) X Pigenopea genotype ICP 3783 (sensitive) suggesting that salinity tolerance is a dominant genetic factor. There was a positive growth response in pigeonpea genotypes with increasing calcium levels in the medium during salinity. The differences between tolerant and sensitive genotypes were maintained irrespective of the external calcium and sodium levels within a given salinity level (6 or 8 dS/m). The symbiotic ability of pigeonpea under saline conditions varied depending on the rhizobial strains, with IC 3087 and IC 3506 being more efficient than IC 3024, IC 3484 and IC 3195.

Key Words: Cajanus cajan, Salinity tolerance, Wild relatives, Physiological mechanisms, Rhizobium, Symbiotic nitrogen fixation, Inheritance.

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