Journal of Experimental Botany, Vol. 41, No. 231, pp. 1263–1269, October 1990

Effect of Salinity on Growth, Nodulation and Nitrogen Yield of Chickpea (*Cicer arietinum* L.)

E. A. E. ELSHEIKH[1] and M. WOOD[2]

Department of Soil Science, The University of Reading, London Road, Reading RG1 5AQ, UK

Received 29 January 1990

ABSTRACT

Chickpea cultivar ILC 482 was inoculated with salt-tolerant *Rhizobium* strain Ch191 in solution culture with different salt concentrations added either immediately with inoculation or 5 d later. The inhibitory effect of salinity on nodulation of chickpea occurred at 4·0 dS m^{-1} (34·2 mol m^{-3} NaCl) and nodulation was completely inhibited at 7 dS m^{-1} (61·6 mol m^{-3} NaCl); the plants died at 8 dS m^{-1} (71·8 mol m^{-3} NaCl).

Chickpea cultivar ILC 482 inoculated with *Rhizobium* strain Ch191^{spcstr} was grown in two pot experiments and irrigated with saline water. Salinity (NaCl equivalent to 1–4 dS m^{-1}) significantly decreased shoot and root dry weight, total nodule number per plant, nodule weight and average nodule weight. The results indicate that *Rhizobium* strain Ch191 forms an infective and effective symbiosis with chickpea under saline and non-saline conditions; this legume was more salt-sensitive compared to the rhizobia, the roots were more sensitive than the shoots, and N_2 fixation was more sensitive to salinity than plant growth.

Key words: *Cicer arietinum*, nodulation, N_2 fixation, *Rhizobium*, salinity.

INTRODUCTION

Chickpea (*Cicer arietinum*) is very sensitive to soil salinity (Lauter and Munns, 1986); irrigation with saline water of 8·3 dS m^{-1} caused a 61·6% loss in yield (Dravid and Goswami, 1987). However, the response by plants to salinity is affected by a number of factors including air pollution, soil fertility, fertilizer application, soil physical conditions, temperature, and relative humidity (Mass, 1986; Lauter and Munns, 1987).

Unsuccessful symbiosis under salt-stress may be due to failure in the infection process due to the effect of salinity on the establishment of rhizobia (Rai and Prasad, 1983; Singleton and Bohlool, 1984). Lakshmi-Kumari, Singh, and Subbarao (1974) working with lucerne (*Medicago sativa*) found that 70 to 100 mol m^{-3} NaCl (8·1 to 11·6 dS m^{-1}) caused a reduction in the number of root hairs; root hair infections were reduced to a minimum by only 35 mol m^{-3} NaCl (4·1 dS m^{-1}). Reduction of nodulation in soybean (*Glycine max*) under saline conditions was attributed to the shrinkage of the root hairs (Tu, 1981). Yousef and Sprent (1983) showed that NaCl affected nodulation and they concluded that there may also be effects on infection. The proportion of root hairs containing infection threads was reduced by 30% under 100 mol m^{-3} NaCl (11·6 dS m^{-1}) (Zahran and Sprent, 1986).

There have been only a few studies (Balasubramanian and Sinha, 1976; Lauter, Munns, and Clarkin, 1981) on the effects of salinity on growth, nodulation or nitrogen fixation by chickpea. The aim of this report was (a) to determine the effect of salinity on the nodulation of chickpea in solution culture and (b) to assess the effect of a continuous supply of salinity on plant growth, nodulation and nitrogen fixation of chickpea inoculated with salt-tolerant *Rhizobium* in soil.

MATERIALS AND METHODS

Rhizobium

Rhizobium sp. (*Cicer*) strain 2-ICAR-UNK-Ch-191 (Ch191) was obtained from the International Centre for Agricultural Research in the Dry Areas (ICARDA). A mutant (Ch191^{spcstr}) was isolated which was resistant to 250 μg cm^{-3} streptomycin sulphate and 250 μg cm^{-3} spectinomycin dihydrochloride as described by Elsheikh and Wood (1990). The strains were

[1] Present address: Department of Biochemistry and Soil Science, Faculty of Agriculture, Shambat, Sudan
[2] To whom correspondence should be addressed.

© Oxford University Press 1990

maintained at 4 °C on yeast extract mannitol (YEM) agar slopes incorporating 3·0 g dm^{-3} $CaCO_3$ (Vincent, 1970). A defined arabinose–galactose–glutamate medium, was used for preparing inoculants in all experiments as previously described (Wood and Cooper, 1988). Chickpea cultivar ILC 482 was obtained from ICARDA.

Solution culture experiments

Sterile N-free nutrient solution (Cooper, 1978) was dispensed in sterile boiling tubes (20 × 7·5 cm) which were closed with cotton wool bungs. One pre-germinated, surface-sterilized seed (0·2% $HgCl_2$ for 3 min followed by five rinses in distilled water) was grown in each tube. A sterile mixture of 100 mol m^{-3} NaCl, 40 mol m^{-3} Na_2SO_4, 3 mol m^{-3} $MgCl_2.6H_2O$ and 14 mol m^{-3} $CaSO_4$ was added to the sterile N-free solution to give the following values (dS m^{-1}): 4·0, 5·0, 6·0, 7·0, or 8·0 (equivalent to 34·2, 46·2, 54·8, 63·3, and 73·6 mol m^{-3} NaCl) in addition to the control (1·5 dS m^{-1}). The tubes were held in blackened boxes with shoots exposed to the atmosphere in a controlled environment growth room at 20 ± 2 °C and were illuminated at 300 μmol m^{-2} s^{-1} (photosynthetically active radiation) for 16 h d^{-1}. Extra sterile N-free solution was added every 3 d. Three replicates were included per treatment. Plants were checked daily for the presence of nodules for 30 d.

Two experiments were carried out. In the first experiment the inoculum of *Rhizobium* strain Ch191 (10^5–10^6 cfu cm^{-3}) was added immediately to chickpea cultivar ILC 482 whereas the salt treatment started 5 d after transplanting to give the required level. In the second experiment both the salt and the inoculum were added 5 d after transplanting.

Pot experiment (1) Effect of salinity on nodulation in soil

Chickpea cultivar ILC 482 was grown in Rowland series soil (1·0 kg in 13·5 cm diameter pots). Four salinity levels (mixture of NaCl and $CaCl_2$ 0·25 Ca:Na on molar basis; Mg salts were not added because they enhance soil dispersion in the presence of Na and Ca salts) of 0, 1, 3, and 4 dS m^{-1} at 25 °C (equivalent to 0, 8·6, 25·7, and 34·2 mol m^{-3} NaCl, respectively) were used for irrigation of chickpea. *Rhizobium* strain Ch191^{spcstr} (10^5–10^6 cfu g^{-1} soil) was used for inoculating chickpeas immediately after transplanting whereas the salt was added in the irrigation water which started 3–5 d after transplanting. Three replications per treatment were kept in a glasshouse (22 ± 3 °C with 14–15 daylight hours) in April/May 1988.

The plants were harvested every week for 4 weeks. Harvesting started one week after the start of the salt treatment. Dry weights of shoots (leaves and stems) and roots were determined, as well as nodule dry weights and average nodule weights (for the last harvest only) and nodule sizes (divided into three groups: small, medium and large with nodule diameter of < 1 mm, 1–2 mm, and > 2 mm, respectively).

Pot experiment (2) Effect of salinity on plant growth and N yield

The previous pot experiment was repeated except that three salinity levels, 0, 5·0, and 10·0 dS m^{-1} at 25 °C (equivalent to 0, 51·3, and 105·9 mol m^{-3} NaCl, respectively) were used. Irrigation with saline water continued for 3 weeks and thereafter the plants received only tap water until the end of the experiment.

Plants were harvested 4, 6 or 8 weeks after starting the salt treatment. Dry weights and nitrogen content (Kjeldahl digestion followed by colorimetric determination of ammonium using a Chem lab autoanalyser) of shoots (leaves and stems) and roots were determined, as well as total nodule number per plant, and average nodule weight per plant, and nodule size.

The amount of N_2 fixed was estimated by N difference after 8 weeks, i.e. the difference in the N yield between inoculated (*I*) and uninoculated (*U*) plants. In order to compare between salt treatments this value was expressed as a percentage of the N yield for the uninoculated plants, $100(I-U)/U$.

RESULTS

Solution culture experiment

The total number of nodules on chickpea plants was reduced as salinity increased. This was the case after 11 d

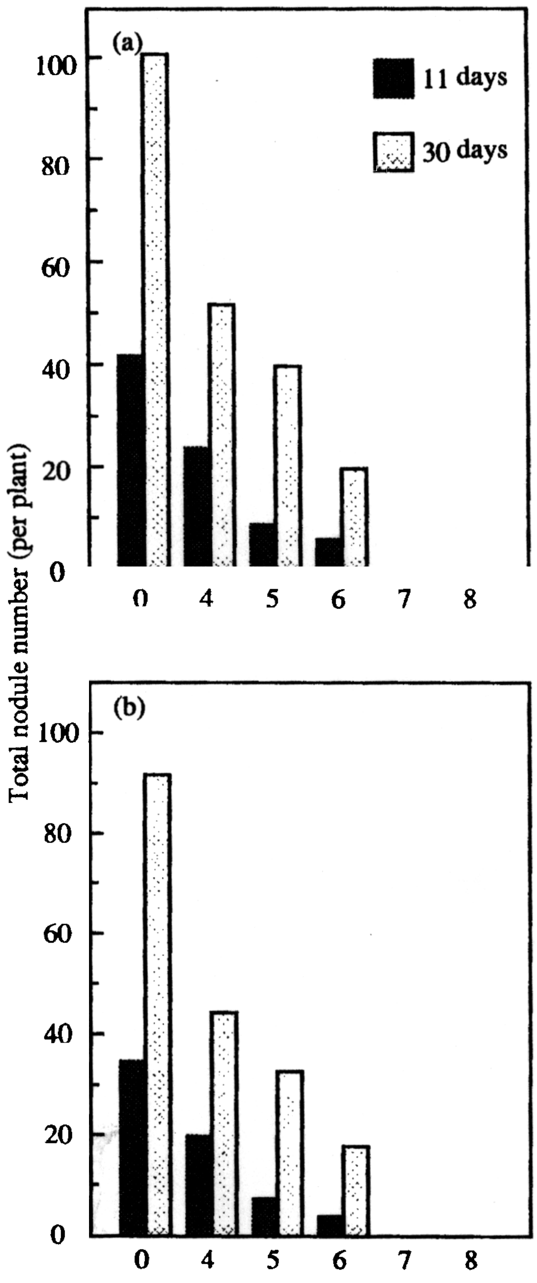

FIG. 1. The effect of salinity (mixture of salts) on nodulation of chickpea cultivar ILC 482 in solution culture using *Rhizobium* strain Ch191. (a) Inoculum was added immediately and salt added after 5 d, (b) inoculum and salt were added 5 d after transplanting. Three replicates per mean.

and 30 d from inoculation (Fig. 1). Nodulation was completely inhibited by 7 dS m^{-1} (61·6 mol m^{-3} NaCl) and the plants died at 8 dS m^{-1} (71·8 mol m^{-3} NaCl).

The inhibitory effect of salt on nodulation of chickpea appeared at the lowest salt level of 4·0 dS m^{-1} (34·2 mol m^{-3} NaCl) and became more inhibitory with increase in salt concentration. The reduction in nodulation in the first experiment after 30 d were 51%, 60%, 80%, 100%, and 100% for 4, 5, 6, 7, and 8 dS m^{-1}, respectively (equivalent to 34·2, 46·2, 54·8, 63·3, and 73·6 mol m^{-3} NaCl, respectively). In the second experiment the reduction was 50%, 64%, 80%, 100%, and 100% for the same salt concentrations, respectively.

In the first experiment, in which the inoculum was added immediately but the salt was added 5 d after transplanting, plants under stress nodulated slightly better than the second experiment in which both salt and the inoculum were added 5 d after transplanting.

Pot experiment (1)

Shoot and root weight: In this experiment salinity significantly reduced the dry weights of both shoots ($P<0·0001$) and roots ($P<0·001$) of inoculated and uninoculated plants (data not shown). The inhibitory effect of salt was apparent after 3 weeks from salt treatment since no significant difference was observed in the first and the second weeks. The results show that this cultivar, like many other chickpea cultivars is sensitive to salinity (Lauter and Munns, 1986). Roots appear to be more sensitive to salinity than shoots even at very low salinity levels of 1·0 dS m^{-1} (8·6 mol m^{-3} NaCl). Salinity levels of 3 and 4 dS m^{-1} caused a significant reduction in dry weights of both shoots and roots. Inoculation had no effect on the dry weights of both shoots and roots.

Nodule number and size: No nodules were found on the roots of chickpea plants in all uninoculated control treatments. For inoculated plants salinity reduced the total nodule number per pot significantly ($P<0·001$) (Fig. 2a). A reduction of 13%, 60%, and 79% in nodule number was caused by salinity levels of 1, 3, and 4 dS m^{-1}, respectively. In general, the total nodule number increased with time in all inoculated treatments.

The nodules formed in the first week after starting the salt treatment (10–12 d after inoculation) were small in size (Fig. 2a). There were no significant differences between nodule sizes formed in the second and third weeks. In the last harvest (week four) only the total number of large size nodules were significantly reduced by salinity.

Nodule weight: The total nodule weight per plant, after four weeks, was significantly decreased ($P<0·05$) by salinity (Fig. 2b). A reduction of 29·2%, 80%, and 83·4% in nodule weight was caused by salinity levels of 1, 3, and 4 dS m^{-1}, respectively. Average individual nodule weights decreased with increase in salinity level; they were 1·40, 1·35, 0·94, and 0·91mg per nodule for 0, 1, 3, and 4 dS

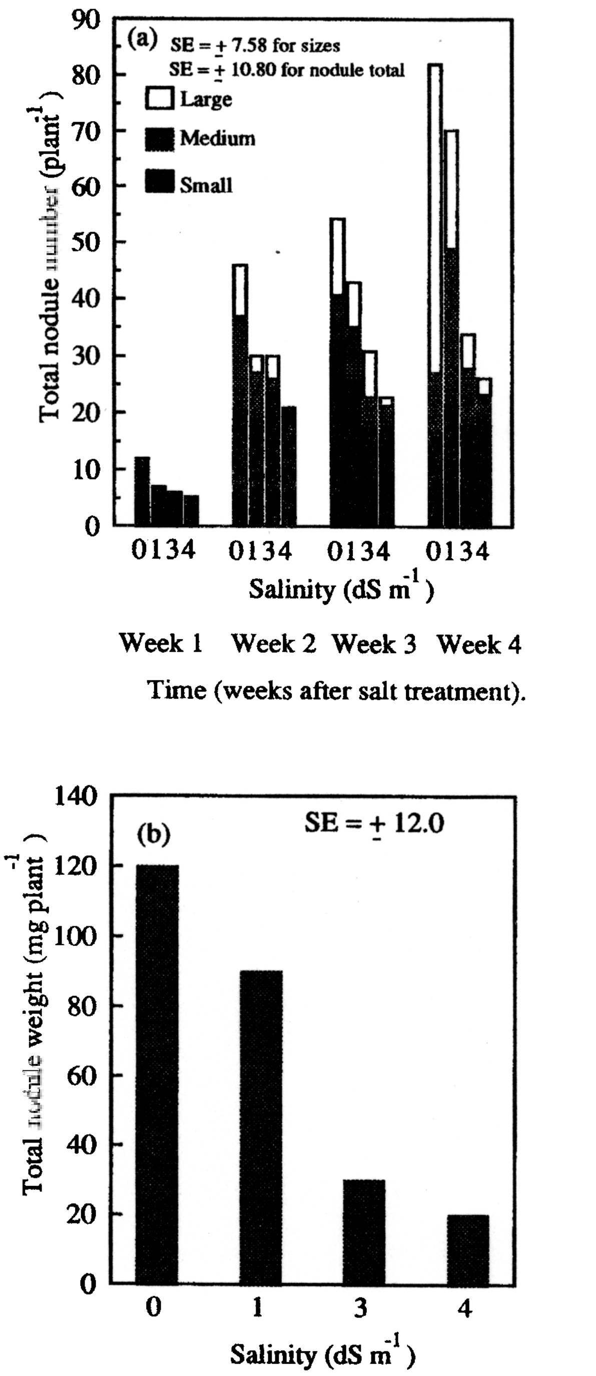

FIG. 2. The effect of salinity (NaCl + $CaCl_2$) on (a) total nodule number and nodule size and (b) nodule weight (after 4 weeks only) on chickpea cultivar ILC 482 inoculated with *Rhizobium* strain Ch191^{spcstr}. Three replicates per treatment (experiment 1).

m^{-1}, respectively. This was reflected in the smaller size nodules formed at the higher salt concentrations.

Pot experiment (2)

Shoot and root weights: In this experiment salinity significantly reduced the dry weights of both shoots and roots ($P<0·0001$) of inoculated and uninoculated chickpea plants (Fig. 3). The inhibitory effect of salt on shoot and root dry weights was apparent after 6 weeks from the start of treatment; plant weights for all salt treatments were significantly different after 6 weeks and 8 weeks. Chickpea plants receiving 10·0 dS m^{-1} survived for only 4 weeks. These results are consistent with the results in pot experiment (1) and confirm that this cultivar is sensitive to salinity.

Inoculation significantly increased the dry weights of both shoots ($P<0{\cdot}0005$) and roots ($P<0{\cdot}0001$) of chickpea plants receiving the 0 and 5·0 dS m^{-1} (51·3 mol m^{-3} NaCl) treatments (Fig. 3).

Nodule number and size: No nodules were found on the roots of chickpea plants in all uninoculated control treatments. Salinity reduced the total nodule number per inoculated plant significantly ($P<0{\cdot}01$) (Fig. 4a). The total nodule number increased with harvest time for the plants receiving 0 or 5·0 dS m^{-1} (51·3 mol m^{-3} NaCl).

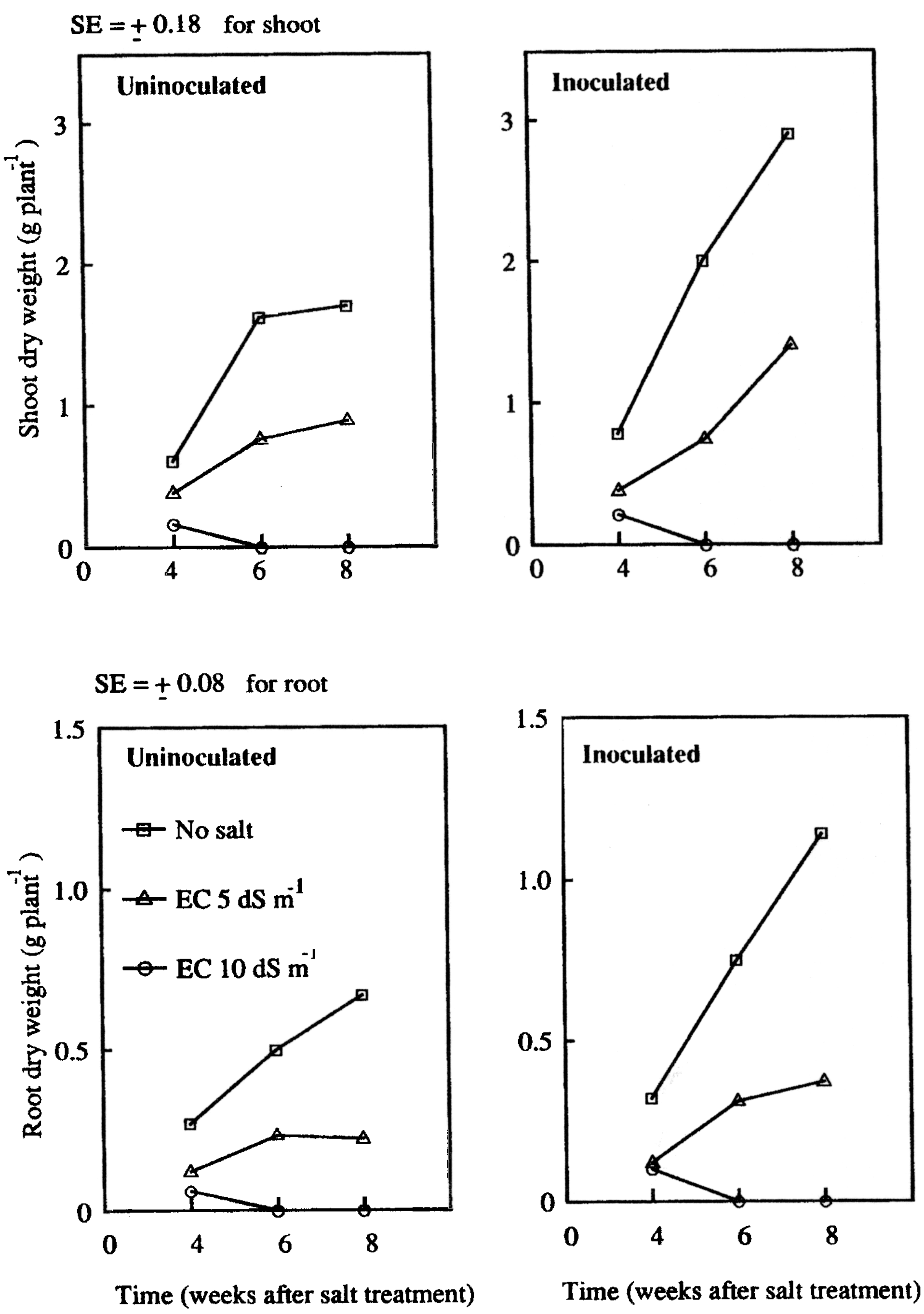

FIG. 3. The effect of salinity ($NaCl+CaCl_2$) on shoot and root dry weight of chickpea cultivar ILC 482 either uninoculated or inoculated with *Rhizobium* strain Ch191$^{spc\,str}$. Three replicates per treatment (experiment 2).

After 8 weeks, nodulation was reduced by 60% on plants receiving 5·0 dS m^{-1} (51·3 mol m^{-3} NaCl). Salinity of 5·0 dS m^{-1} (51·3) significantly decreased the number of small, medium and large nodules compared to plants receiving no salt (Fig. 4a). Plants receiving the highest salinity treatment (10·0 dS m^{-1}; 105·9 mol m^{-3} NaCl), although they survived for only 4 weeks, were able to produce nodules on their reduced roots. Total nodule weight per plant followed a similar pattern to total nodule number per plant (Fig. 4b).

Shoot and root nitrogen: Inoculation and harvest time significantly increased ($P < 0·0001$) the total N content in both shoots and roots of chickpea (Table 1). However, salinity significantly decreased ($P < 0·0001$) the total N of both shoots and roots. The N benefit due to inoculation ($I - U$) was greater for shoots than roots at 0 and 5·0 dS m^{-1}, and was significantly decreased by salinity (Table 1).

DISCUSSION

A favourable rhizosphere environment is of great importance to the interaction between root hairs and *Rhizobium* (*Bradyrhizobium*) as it not only encourages the growth and multiplication of rhizobia but also ensures the healthy development of root hairs. The former increases the inoculum potential and the latter provides infection sites (Tu, 1981). Any environmental factor which affects those processes is also likely to affect infection and nodulation.

The dry weight of shoots and roots of inoculated and uninoculated chickpea cultivar ILC 482 were significantly reduced by salinity in both pot experiments. Inoculation increased the dry weight of both shoots and roots of pot experiment (2), yet no effect was observed on plant growth in experiment (1), probably because of the short time (4 weeks) which was not long enough for the nodules to contribute to enhanced plant growth. Salinity has been reported to reduce shoot and root weights in legumes, e.g. chickpea (Lauter and Munns, 1987), soybean (*Glycine max*) (Singleton and Bohlool, 1984; Grattan and Mass, 1988), and faba bean (*Vicia faba*) (Yousef and Sprent, 1983; Zahran and Sprent, 1986). For *Vigna radiata* at maturity (65 d) 95% of the plants survived at 7·5 dS m^{-1} (68·0 mol m^{-3} NaCl), however, all plants died at 10·0 dS m^{-1} (90·0 mol m^{-3} NaCl) regardless of the presence or absence of inoculation (Hafeez, Aslam, and Malik, 1988). Results reported here confirm that chickpea cultivar ILC 482 is sensitive to saline conditions.

The sensitivity to salt by chickpea may be linked to the inhibition of the plant growth through accumulation of Na in the shoots, due to the inability of the plant to decrease transpiration upon the addition of salt (Lauter and Munns, 1986). The plants have an aqueous glandular exudate which persists on the leaves and stems, evidently permitting considerable water loss whether salt-stress is present or absent (Lauter and Munns, 1987). Excessive accumulation of Na adversely affects enzymatic activity, photosynthesis rate, and the translocation and further utilization of photosynthates.

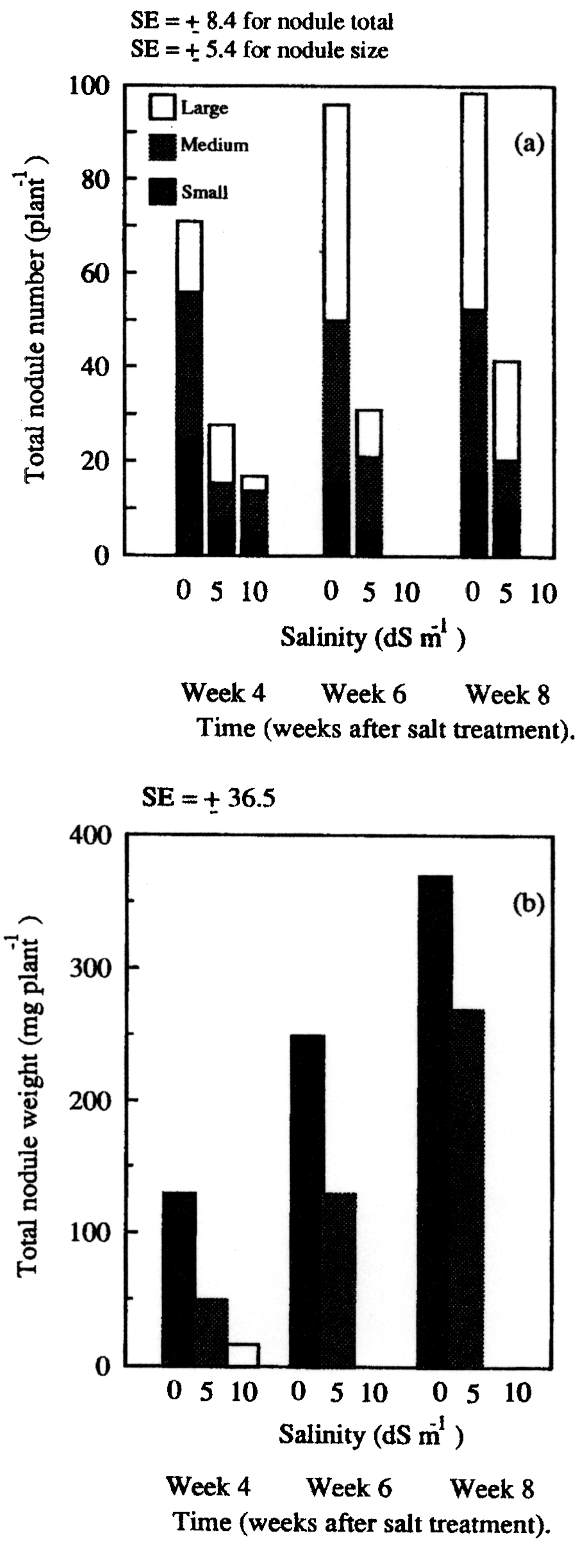

FIG. 4. The effect of salinity (NaCl + $CaCl_2$) on (a) total nodule number and nodule size and (b) nodule weight on chickpea cultivar ILC 482 inoculated with *Rhizobium* strain $Ch191^{spcstr}$. Three replicates per treatment (experiment 2).

In all experiments, salinity significantly reduced the

TABLE 1. *The effect of salinity (NaCl+ CaCl$_2$) on total N (mg plant^{-1}) in shoots and roots of chickpea cultivar ILC 482 either uninoculated (U) or inoculated (I) with* Rhizobium *sp.* (Cicer) *strain Ch191^{spcstr}*

Three replicates per treatment.

(a) Shoots (s.e. $\pm$0·6)

Harvest	Inoculation	Salt level (dS m^{-1})		
		0·0	5·0	10·0
4 weeks	U	6·0	4·2	2·1
	I	12·8	4·8	2·4
6 weeks	U	22·4	10·4	0·0
	I	33·0	12·6	0·0
8 weeks	U	27·2	15·3	0·0
	I	49·0	21·6	0·0
I − U (8 weeks)		21·8	6·3	0·0
100(I − U)/U		80·1	41·2	0·0

(b) Roots (s.e. = $\pm$0·47)

Harvest	Inoculation	Salt level (dS m^{-1})		
		0·0	5·0	10·0
4 weeks	U	2·1	1·8	1·6
	I	4·1	2·3	1·8
6 weeks	U	6·5	2·0	0·0
	I	11·6	4·6	0·0
8 weeks	U	9·5	3·6	0·0
	I	19·2	7·0	0·0
I − U (8 weeks)		10·2	1·9	0·0
100(I − U)/U		107·4	52·8	0·0

total nodule number per plant. In general, the total nodule number per plant in experiment (2) increased with time in all treatments, indicating the tolerance of *Rhizobium* strain Ch191 to salinity. These results are in agreement with the results of Hafeez *et al.* (1988) who reported that the nodulation of *Vigna radiata* was reduced by about half at a salinity level of 5·0 dS m^{-1} when compared to 1·4 dS m^{-1}. However, they also found that nodulation was completely depressed when salinity was raised to 10·0 dS m^{-1}, regardless of the plant growth stage. In the experiments reported here nodulation was recorded at 10·0 dS m^{-1} at the 4 week harvest in experiment (2) (Fig. 4a).

Nodule formation by chickpea was adversely affected by even low levels of salinity (1·0 dS m^{-1}). In general, the total nodule number increased with time in the control and all salt treatments. Wilson (1970) reported that the development of new nodules by soybean and nitrogen fixation by the existing nodules were greatly inhibited by salinity, with a resulting decline in plant nitrogen content. The failure of nodule formation at high salinity might be attributed to shrinkage of root hairs, consequently, the reduction in plant growth under conditions of high salinity could only be partly accounted for by the reduction or failure in nodulation (Tu, 1981). The processes of nodule initiation in soybean was reported to be extremely sensitive to NaCl. A reduction in nodule number and weight of 50% occurred with 26·6 mol m^{-3} NaCl (3·1 dS m^{-1}) in the rooting medium (Singleton and Bohlool, 1984). 20 mol m^{-3} NaCl (2·3 dS m^{-1}) inhibited nodulation of chickpea plants inoculated with four different *Rhizobium* strains by 16–20% (Lauter *et al.*, 1981). In this study, nodulation of chickpea was reduced by more than 50% at 34·2 mol m^{-3} NaCl (4·0 dS m^{-1}) in solution culture and in soil (Fig. 1).

The average nodule weight in experiment (2) increased with an increase in salinity level. Average nodule weight of faba bean was found to increase with salinity (Yousef and Sprent, 1983), yet Zahran and Sprent (1986) found a reduction in average nodule weight using the same salinity levels. Such differences were attributed to differences in the environmental conditions (Sprent, Stephens, and Rupela, 1988). An increase in average nodule weight with increase in salinity level was also reported for chickpea (Balasubramanian and Sinha, 1976; Lauter *et al.*, 1981); this increase may partly compensate for reduced specific nitrogenase activity (Yousef and Sprent, 1983). In these experiments the amount of N_2 fixed was reduced by salinity (Table 1). When expressed as a proportion of the N yield of the uninoculated plants N_2 fixation appeared more sensitive to salinity than plant growth (Table 1).

Overall, the results reported here show that the host legume cultivar was more sensitive to salinity than the *Rhizobium* symbiont and thus there is a need for highly salt-tolerant chickpea cultivars. Salinity significantly reduced shoot and root dry weights, nodule number, nodule weight, total plant N, and N_2 fixation for chickpea. The results indicate that *Rhizobium* strain Ch191 was able to form an effective symbiosis with chickpea cultivar ILC 482 under saline and non-saline conditions. However, N_2 fixation was more sensitive than plant growth to salinity.

ACKNOWLEDGEMENT

We thank the Sudanese Government for financial support. We are also grateful to Dr L. Materon (ICARDA) for supplying cultures of chickpea rhizobia.

LITERATURE CITED

BALASUBRAMANIAN, V., and SINHA, S. K., 1976. Nodulation and nitrogen fixation in chickpea (*Cicer arietinum* L.) under salt stress. *Journal of Agricultural Science, Cambridge*, **87**, 465–6.

COOPER, J. E., 1978. A method for testing *Rhizobium* effectiveness at low pH. *Soil Biology and Biochemistry*, **10**, 81–3.

ELSHEIKH, E. A. E., and WOOD, M., 1990. Antibiotic-resistant mutant of chickpea and soybean rhizobia under saline stress. *Plant and Soil.* Submitted.

DRAVID, M. S., and GOSWAMI, N. N., 1987. Effect of salinity, fertility and variety on growth and nutrient uptake by chickpea (*Cicer arietinum* L.). *Journal of Nuclear Agricultural Biology*, **16**, 69–72.

GRATTAN, S. R., and MASS, E. V., 1988. Effect of salinity on phosphate accumulation and injury in soybean: 1. Influence of CaCl$_2$/NaCl ratios. *Plant and Soil*, **105**, 25–32.

HAFEEZ, F. Y., ASLAM, Z., and MALIK, K. A., 1988. Effect of salinity and inoculation on growth, nitrogen fixation and nutrient uptake of *Vigna radiata* (L.) Wilczek. Ibid. **106**, 3–8.

LAKSHMI-KUMARI, M., SINGH, C. S., and SUBBARAO, N. S., 1974. Root hair infection and nodulation in lucerne *Medicago sativa* L. as influenced by salinity and alkalinity. Ibid. **40**, 261–8.

LAUTER, D. J., and MUNNS, D. N., 1986. Salt resistance of chickpea genotypes in solutions salinized with NaCl or Na_2SO_4. Ibid. **95**, 271–9.

——— 1987. Salt sensitivity of chickpea during vegetative growth and at different humidities. *Australian Journal of Plant Physiology*, **14**, 171–80.

——— and CLARKIN, K. L., 1981. Salt response of chickpeas influenced by N supply. *Agronomy Journal*, **73**, 961–6.

MASS, E. V., 1986. Salt tolerance of plants. *Applied Agricultural Research*, **1**, 12–26.

RAI, R., and PRASAD, V., 1983. Salinity tolerance of *Rhizobium* mutants: growth and relative efficiency of symbiotic nitrogen fixation. *Soil Biology and Biochemistry*, **15**, 217–19.

SINGLETON, P. W., and BOHLOOL, B. B., 1984. Effect of salinity on the nodule formation by soybean. *Plant Physiology*, **74**, 72–6.

SPRENT, J. I., STEPHENS, J. H., and RUPELA, O. P., 1988. Environmental effects on nitrogen fixation. In *World crops: Cool season food legumes*. Ed. R. J. Summerfield. Pp. 801–10.

TU, J. C., 1981. Effect of salinity on *Rhizobium*-root hair interaction, nodulation and growth of soybean. *Canadian Journal of Plant Science*, **61**, 231–9.

VINCENT, J. M., 1970. *A manual for the practical study of root nodule bacteria*. Blackwell Scientific Publications, Oxford.

WILSON, J. R., 1970. Response to salinity in glycine. VI. Some effects of a range of short-term salt-stresses on the growth, nodulation, and nitrogen fixation of *Glycine whightii* (Formerly *javanica*). *Australian Journal of Agricultural Research*, **21**, 571–82.

WOOD, M., and COOPER, J. E., 1988. Acidity, aluminium and multiplication of *Rhizobium trifolii*: effects of initial inoculum density and growth phase. *Soil Biology and Biochemistry*, **20**, 83–7.

YOUSEF, A. N., and SPRENT, J. I., 1983. Effects of NaCl on growth, nitrogen incorporation and chemical composition of inoculated and NH_4NO_3 fertilized *Vicia faba* (L.) plants. *Journal of Experimental Botany*, **34**, 941–50.

ZAHRAN, H. H., and SPRENT, J. I., 1986. Effects of sodium chloride and polyethylene glycol on root-hair and nodulation of *Vicia faba* L. plants by *Rhizobium leguminosarum*. *Planta*, **167**, 303–9.