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GENOMIC RELATIONSHIPS IN OILSEED BRASSICAS WITH RESPECT TO SALT TOLERANCE – PHOTOSYNTHETIC CAPACITY AND ION RELATIONS

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Abstract

Salt tolerance of three amphidiploid species, *Brassica napus*, *B.carinata* and *B.juncea* with respect to their diploid parents, *B.oleracea*, *B.nigra* and *B.campestris* was investigated. Twenty three-day old plants of these six species were subjected for 28 days to salinized sand culture containing 0, 100 or 200 mol NaCl m^{-3} in Hoagland's nutrient solution. All three amphidiploids produced significantly greater shoot fresh and dry matters, and seed yield than their respective diploid parents under saline conditions, *B.napus* being the highest followed by *B.carinata* and *B.juncea* of all the species. Of the diploid parents *B.nigra* was the lowest followed by *B.oleracea* in terms of relative shoot biomass since the plants of the former species subjected to the highest salt concentration did not survive till maturity. A close association was found between growth and CO_2 assimilation rate (A) for all species differing in degree of salt tolerance. Stomatal conductance (g_s) was reduced due to salt stress in all the species but this variable had no significant correlation with assimilation rate. However, the amphidiploid species had significantly greater photosynthetic rate, water use efficiency (A/E), intrinsic water use efficiency (A/g_s) than those of their diploid parents. Parallels were drawn between data for ion accumulation in different plant parts and salt tolerance of the *Brassica* species. All three diploid parents had significantly higher Na^+ but lower K^+ in the shoots at all external salt regimes as compared with that of amphidiploid species. The same pattern was observed for root K^+. The shoot Ca^{2+} decreased considerably in *B.nigra* and *B.oleracea* and increased in *B.napus* at the highest salt regime, whereas in the other species no effect of salt was observed on shoot Ca^{2+}concentration. Shoot Cl^- was the lowest in the salt tolerant *B.napus* of all the species, whereas the difference among the other species for this ion was not consistent. All three amphidiploids maintained significantly higher K/Na and Ca/Na ratios in the shoots compared with the diploid species. In conclusion, high salt tolerance of the amphidiploids was associated with a high assimilation rate, water use efficiency, intrinsic water use efficiency and shoot K/Na and Ca/Na ratios, and partial exclusion of Na^+ from the shoots. In contrast, there was little association of the tolerance of these species with stomatal conductance, leaf water potential or transpiration rate (E). The salt tolerance trait in amphidiploid species seemed to have been inherited from the diploid species *B.campestris* and *B.oleracea* with genomes A and C, respectively.

Introduction

Brassica oilseed species are third most important source of vegetable oil in the world (Downey, 1990; Kumar, 1995). However, the productivity of these crops is adversely affected in arid and semi-arid regions because of high amounts of soluble salts, which is a distinctive characteristic of the soils of those regions (Munshi et al., 1986; Ashraf and McNeilly, 1990). Nonetheless, such salt affected soils can be economically utilized by growing salt tolerant species/cultivars.

Salt tolerance is very complex in most plant species because salt stress is known to cause tissue dehydration, ion toxicity, nutritional imbalance, or a combination of these effects (Greenway and Munns, 1980; Gorham et al., 1991; Ashraf, 1994; Dubey, 1997; Yeo, 1998; Carvajal et al., 1999; Makela et al., 1999). There are numerous mechanisms, at cellular, tissue, organ, or whole plant levels. Some traits may only be functional at one time in a particular species. In addition, the effect of one mechanism may mutually exclude the effect of the others at certain stages of development (Gorham et al., 1991; Yeo, 1998; Carvajal et al., 1999). The situation becomes even more complex when polyploid species are compared with their respective diploid ancestors, the former generally withstanding adverse environmental factors better than the latter (Stebbins, 1966). In earlier screening of four *Brassica* species for salt tolerance, *B. napus* and *B. carinata* were salt-tolerant compared with *B. campestris* (Ashraf and McNeilly, 1990; Malik, 1990; He and Cramer, 1992; Kumar, 1995). *B. juncea*, an amphidiploid, was intermediate in salt tolerance. In this paper an analytical approach was carried out to identify relationships between amphidiploid and diploid *Brassica* species with respect to salt tolerance as has earlier been done for wheat (Shah *et al.,* 1987).

From the cytogenetical relationships of the *Brassica* species (Hemingway, 1976: McNaughron, 1976) it is evident that *B. carinata* is an amphidiploid (BBCC, *n* =17) probably arising from *B. oleracea* (CC, *n* = 9) and *B.nigra* (BB, *n* = 8): *B.napus* is an amphidiploid (AACC, *n* =19) of *B.oleracea* and *B. campestris* (AA, *n* = 10), whereas *B. juncea* is an amphidiploid (AABB, *n* = 18) of *B. campestris* and *B. nigra.*

In view of the evolution (Hemingway, 1976; McNaughton, 1976) and degrees of salt tolerance (Ashraf and McNeilly, 1990; He and Cramer, 1992) of *Brassica* species, it is not clear which diploid genome (s) is responsible for enhanced salt tolerance in amphidiploids. Thus our principal objective in undertaking the present study was to affirm whether the salt tolerance trait in the three amphidiploid species was derived from the A, B, or C genome.

Materials and methods

Seed material of the six *Brassica* species, *B.napus* L. (cv Shiralu 99), *B.campestris* L. (cv Toria Selection A), *B.juncea* (L.) Czern. & Coss. (cv KL-18), *B.carinata* A.Br. (cv Peela Raya), *B.oleracea* L. (type Phool ghobi), and *B.nigra* (L.) Koch (a land race) was obtained from the Oil-seed Section, Ayub Agricultural Research Institute Faisalabad, Pakistan.

All seed samples were surface sterilized in 5% sodium hypochlorite solution for 10 min before sowing. In September 1999, three hundred seeds of each species were sown randomly in thoroughly washed sand in plastic containers (40 x 30 x 6 cm) with drainage holes in the bottom. The sand was irrigated on alternate days with 3 l of full strength Hoagland nutrient solution . The experiment was carried out in a naturally-lit glasshouse in the Department of Soil Science, University of Agriculture, Faisalabad where the average photosynthetic photon flux density (PPFD) measured at noon ranged from 425 to 1360 μmol m^{-2} s^{-1}, day/night relative humidity 58/74% and temperature 24/8 °C. After 8 d, six seedlings were transplanted into plastic pots (22.5 cm diameter and 22.5 cm deep) each containing 7.52 kg of well-washed dry sand. All the pots were irrigated for 15 days with full strength Hoagland nutrient solution. Additions of NaCl treatment, 0, 100, or 200 mol m^{-3} in full strength Hoagland nutrient solution were begun 23 d after the start of the experiment.

The experiment was arranged in a completely randomized design with 4 replicates, with three salt treatments, which were increased daily in stepwise aliquots of 50 mol m^{-3} in Hoagland's nutrient solution until the appropriate salt treatments were reached. Treatments continued with the addition of 2 litres of the appropriate solution to each pot twice a week, sufficient to wash through solution already present in the sand as determined from the electrical conductivity of the effluent solution from the pots. Every day 200 ml of distilled water was added to each pot to compensate for evapotranspiration loss. This was sufficient to moisten the sand but did not cause leaching of salts from the pots. After four weeks after the start of salt treatment the following physiological parameters were measured:

Gas exchange characteristics: Measurements of net CO_2 assimilation rate (A), transpiration (E) and stomatal conductance (g_s) were made on fully expanded youngest leaf of each plant using an open system LCA-4 ADC (with single leaf measuring chamber) portable infrared gas analyzer (Analytical Development Company, Hoddesdon, England). Measurements were performed from 9.00 to 11.00 a.m. with the following specifications/adjustments: molar flow of air per unit leaf area 405.4 mmol m^{-2} s^{-1}, atmospheric pressure 99.6 kPa, water vapour pressure into chamber ranged from 11.1 to 12.2 mbar, PPFD at leaf surface was maximum up to 984 μmol m^{-2} s^{-1}, temperature of leaf ranged from 26.8 to 32.3 °C, ambient temperature ranged from 26.6 to 33.3 °C, ambient CO_2 concentration 352 μmol mol^{-1}. Water use efficiency was calculated as CO_2 assimilation rate/transpiration, and intrinsic water use efficiency as CO_2 assimilation rate/stomatal conductance.

After all these measurements, two plants from each pot were harvested. Plant roots were removed carefully from the sand and washed for 2-3 min in distilled water. Plants were separated into shoots and roots. Fresh weights of shoots and roots of all the plant samples were recorded. Samples were then dried at 65 °C for one week and dry weights recorded. Dry material was used for the analysis of ions.

Inorganic elements: For the determination of Na^+, K^+, and Ca^{2+} contents, 50-100 mg of well ground dry material of shoots and roots were digested in 2-3 ml concentrated HNO_3 (Merck) and the Na^+, K^+, and Ca^{2+} in the digests were determined with a flame photometer (Jenway PFP7). For Cl^-, 50-100 mg ground sub-samples of shoots and roots were extracted in 10 ml of distilled deionized water at 80 °C for 4 h. Cl^- concentration was determined with a chloride analyzer (Corning, 925).

Results

Saline growth medium caused a significant reduction ($P \leq 0.001$) in mean dry weight of shoots and seed yield of all six *Brassica* species (Fig. 1), and species differed significantly ($P \leq 0.001$) in growth and yield variables in response to saline growth medium. *B.oleracea* and *B.nigra* were lower in shoot dry weights in both salt treatments compared with the other four species. At the highest salt treatment the other four *Brassica* species did not differ significantly in shoot biomass, although *B.napus* had higher values of shoot dry weights than the other species. The type of *B.oleracea* used was cauliflower and produced no seed, and therefore data for seed yield was only from five species, as seen in Fig. 1. In addition, all the *B.nigra* plants exposed to 200 mol m^{-3} NaCl died before maturity, and there were therefore no highest salt treatment seed yield data. Comparison of species in seed yield (mean and relative seed yield) showed that *B.napus* had the highest seed yield (31%) followed by *B.carinata* (27%), and *B.nigra* (0%), the lowest of all the species under saline conditions. *B.juncea* (19%) and *B.campestris* (19%) were intermediate in seed yield.

Net CO2 assimilation rate (A) of all six species had a decreasing trend with increase in salt concentration of the rooting medium (Fig. 2A). The low shoot biomass producing species, *B.oleracea* and *B.nigra* had significantly lower ($P \leq 0.05$)

assimilation rates than those of the other species for all treatments. The species *B.carinata* was the highest of all the species in assimilation rate at both salt treatments, whereas *B. napus* was as good as *B. campestris* and *B. juncea.*

Stomatal conductance (Fig. 2B) of all six species also decreased significantly with increase in external salt regimes ($P \leq 0.001$) except *B. juncea*. At 100 mol NaCl m^{-3}, *B. nigra* followed by *B. juncea* and *B. napus* had significantly higher stomatal conductance than the other species. At the highest salt regime, *B. nigra* and *B. juncea* were significantly higher in stomatal conductance compared with the other species.

Saline growth medium caused a significant decrease in transpiration rate in all six species. At 100 mol NaCl m^{-3}, *B. campestris* and *B. napus* had lower transpiration than that of the other species (Fig. 3C). At the highest salt treatment, *B. campestris, B. carinata* and *B. oleracea* had lower transpiration than that of the other three species. *B. juncea* was the highest and *B. campestris* the lowest in transpiration rate of all the species at both salt treatments.

Water use efficiency (A/E) remained unchanged in all the species except *B. carinata* (Fig. 3E). The species *B. nigra* was the lowest of all the species in water use efficiency at both salt treatments. At the highest salt level, *B. carinata* was the highest of all species in water use efficiency.

Relative intercellular CO_2 concentration (C_i/C_a = intercellular CO_2 concentration/ambient CO_2 concentration) decreased with increase in external salt concentration in all species except *B.juncea* and *B.nigra* in which it remained almost unaffected with increase in salt level of the growth medium (Fig. 4D). At 100 mol m^{-3} NaCl, *B.campestris* was the highest whereas at 200 mol m^{-3} NaCl *B. juncea* the highest of all the species in relative intercellular CO_2 concentration.

Intrinsic water use efficiency (A/g_s) increased in *B. carinata,* and *B. napus* with increase in external salt concentration, but it remained unaffected in the remaining four species (Fig. 4F). The species *B. carinata* was the highest and *B. napus* the second highest of all species in intrinsic water use efficiency at the highest salt level. At the same salt treatment, *B. nigra* was the lowest of all species except *B. juncea* in intrinsic water use efficiency.

Although shoot Na^+ concentration increased considerably in all six *Brassica* species as external salt concentration increased, there was a significant difference among the species (Fig. 5). All three amphidiploids had significantly lower shoot Na^+ compared with the diploids at both salt treatments. However, root Na^+ was maximum in *B.carinata* at 100 mol m^{-3} NaCl and in *B.nigra* at the highest salt treatment of all the species (Fig. 5).

Shoot K^+ concentrations of all three amphidiploids were significantly higher than those of the diploid species under non-saline and saline conditions (Fig. 6), and this occurred in the roots as well.

There was no significant effect of NaCl on shoot Ca^{2+} concentration and no significant species differences (Fig. 7). In contrast, there was a significant effect of NaCl on root Ca^{2+}, and also a marked difference among the species. The pattern of increase or decrease of root Ca^{2+} in species, which differ in salt tolerance was not consistent. *B.campestris* and *B.juncea* roots contained significantly high Ca^{2+} when grown at both 100 and 200 mol m^{-3} NaCl solutions. *B.carinata* had high Ca^{2+} content when grown at 100 mol m^{-3} NaCl, and in contrast *B. nigra* had high Ca^{2+} when grown at 200 mol m^{-3} NaCl (Fig. 7).

The difference among the amphidiploid and diploid species in Cl^- concentrations of shoots or roots was not consistent at varying external salt concentrations (Fig. 8). At 100 mol m^{-3} NaCl, *B.napus* and *B.oleracea* had significantly lower shoot Cl^- than that of the other four species. In contrast, at 100 mol m^{-3} NaCl, *B.napus* was the lowest of all the species, followed by *B.nigra* containing shoot Cl^-. Root Cl^- concentration was significantly higher in *B.napus* and *B.carinata* than that in the other species at the highest external salt concentration (Fig. 8). At 100 mol m^{-3} NaCl, there was no significant difference between species in root Cl^-, except *B.napus* which had the lowest Cl^- in the roots, other than 200 mol m^{-3} NaCl.

Generally, all the amphidiploid species maintained higher K/Na ratios in both shoots and roots than did the diploid species (Fig. 9). Although statistically non-significant, all three amphidiploids again had higher Ca/Na ratios in the shoots, but this was not evident in the roots of the three diploid species (Fig. 10).

Discussion

The results for shoot biomass and seed yield of the six *Brassica* species subjected to saline conditions clearly depict that all three amphidiploids, *B. napus*, *B. carinata*, and *B. juncea* were salt tolerant compared with their putative diploid relatives, *B. campestris*, *B. oleracea*, and *B. nigra*. The three parental diploid species differed in shoot biomass and seed yield when grown in saline solutions, comparing *B. campestris* (A genome) > *B. oleracea* (C genome) > *B. nigra* (B genome). The amphidiploids appeared to have greater salt tolerance over the diploid species, which had already been shown in different studies (Rana et al., 1980; Ashraf and McNeilly, 1990; Malik, 1990; Kumar, 1995). However, there is little information about their genomic relationship for salt tolerance.

The results for shoot biomass and net CO_2 assimilation rates of all six *Brassica* species differing in salt tolerance can be easily related to some earlier studies in which a close relationship has been found between the two variables, i.e., growth and photosynthetic capacity, in different crop species, e.g., spinach (Robinson et al., 1983), *Phaseolus vulgaris* (Seemann and Critchley, 1985), *Vigna mungo* (Chandra Babu et al., 1985 *Zea mays* (Crosbie and Pearce, 1982), *Gossypium hirsutum* (Pettigrew and Meredith, 1994), *Gossypium barbadense* (Cornish et al., 1991), and asparagus (Faville et al., 1999).

Higher stomatal conductance in plants is known to increase CO_2 diffusion into leaves thereby favouring higher photosynthetic rates. Higher net assimilation rates could in turn favour a higher biomass and higher crop yields (Taiz and Zéiger, 1998). But the results for photosynthetic rate and stomatal conductance presented here for six *Brassica* species do not show any significant relationship (r = 0.43NS), though these two variables declined consistently in all six species with increase in salt concentration of the growth medium. For instance, the salt tolerant amphidiploid species, *B.napus* and *B.carinata* had higher photosynthetic rates compared with the other four species including the two diploid parents, *B.oleracea* and *B.nigra*. But in contrast, the former species were as good as the latter in stomatal conductance. These results are not in agreement with those of Radin et al. (1994) who found that in Pima cotton (*Gossypium barbadense*) higher stomatal conductance favoured higher yields. However, the results can be related to some earlier studies on different crops, in which it was shown that stomatal conductance bears little relationship with photosynthetic rate in cotton (Constable and Rawson, 1980), sunflower (Rawson and Constable, 1980), and faba beans (Melesse and Caesar, 1992).

The reduction in plant growth under salt stress is often mediated through lower photosynthetic rates (Robinson et al., 1983; Seemann and Critchley, 1985; Rawson et al., 1988). However, salt stress perturbs photosynthesis due to either reduced stomatal conductance or inhibition of appropriate metabolic phenomena or combination of both (Robinson et al., 1983; Bowman, 1988). But from the data for relative intercellular CO_2 concentration (C_i/C_a) it is evident that in all *Brassica* species except *B.juncea* the substomatal concentration decreased consistently with increase in external salt concentration. This suggests that the decline in photosynthesis to some extent occurred through stomatal closure. But conversely, in *B.juncea* the relative intercellular CO_2 concentration was considerably higher at the highest external salt regime at which the net assimilation rate was low. This suggests that stomatal conductance was not the major factor effecting photosynthesis in this species.

Although transpiration rate decreased considerably in all *Brassica* species with increased concentration of external salt, the difference among salt tolerant and salt sensitive species in this variable was not consistent. For instance, salt tolerant *B.carianata* was as good as salt sensitive *B.oleracea* and moderately tolerant *B.campestris* in transpiration rate at the highest salt regime. The higher water use efficency of the salt tolerant species *B.carinata* compared with the other *Brassica* species was mainly due to its relatively higher assimilation rates since in the former species water use efficiency increased consistently with increase in external salt concentration whereas it remained unaffected in all the other species. But the higher intrinsic water use efficiency in the two salt tolerant *B.carinata* and *B.napus* at the highest external salt level was due to their higher assimilation rate and lower stomatal conductance compared with those of the other species. Intrinsic water use efficiency and photosyhtesis were thus positively correlated ($r = 0.86$, $P \leq 0.001$) in the *Brassica* species as has already been found in the C_4 dicot *Amaranthus retroflexus* (Sage and Pearcy, 1987) and sugarcane (Ranjith and Meinzer, 1997).

Generally, two types of mechanisms of salt tolerance have been identified in higher plants (Flowers et al., 1977; Greenway and Munns, 1980; Wyn Jones et al., 1984; Ashraf, 1994). In the first mechanism, the growth medium salinity causes specific ion effects on plants, and plants in turn respond by excluding toxic ions such as Na^+ and Cl^- from the leaves by different ways. In the second mechanism, ions absorbed by cells are accumulated in the vacuoles. However, patterns of ion accumulation have been successfully used in discriminating between salt tolerant and salt sensitive species or cultivars (Wyn Jones et al., 1984; Shannon and Grieve, 1999). In the present study, all three amphidiploids partially excluded Na^+ from the shoots and roots, accumulated more K^+, and hence maintained considerably higher tissue K/Na ratios as compared with their diploid parents. This shows that all the amphidiploids discriminated to some extent for K^+ and against Na^+ in ion uptake into the roots, and thereby translocation to the shoots. However, the enhanced K/Na discrimination character in these amphidiploid *Brassica* species does not seem to have an effect on anion concentration in shoots or roots. These results can be related, to some extent, to the earlier findings of Gorham *et al.* (1991) in which the enhanced K/Na discrimination character was found the D genome (*Aegilops squorrosa*) in hexaploid wheat. Although we were not able to get seed of the actual diploid parents of the three amphidiploids, the great difference in salt tolerance between diploids and amphidiploids examined in this study allowed us to draw some inferences with respect to their genomic relationship. However, in the present study if parallels are drawn between amphidiploid and diploid species with respect to enhanced K/Na discrimination, it is evident that all these diploid parents had similar values of tissue K/Na ratios when growing under saline conditions. It is thus possible that the enhanced K/Na discrimination trait in the amphidiploids may have been derived almost uniformly from the three genomes, A, B, and C. In contrast however, if the degree of salt tolerance among the amphidiploids is compared with that of the diploid species on the basis of their growth performance in the saline medium, it is amply clear that of the diploids, *B.campestris* is relatively salt tolerant, *B.nigra* salt sensitive because all of the plants died before its reproductive phase, when they had been grown in 200 mol m^{-3} NaCl solution, and *B.oleracea* intermediate in salt tolerance. In addition, of the amphidiploids, *B.napus* was salt tolerant followed by *B.carinata* and *B.juncea.*

If the genomic relationships of these species are drawn, *B.napus* (AC genome) was derived from the hybridization of *B.campestris* (A genome carrying salt tolerance trait) and *B.oleracea* (C genome, moderately salt tolerant). The parents of *B.juncea* (AB genome) are *B.campestris* (A genome) and *B.nigra* (B genome, salt sensitive) and those of *B.carinata* (BC genome) are *B.oleracea* (C genome, moderately salt tolerant) and *B.nigra* (B genome, salt sensitive). From the data presented here, the information presented, it appears likely that the most salinity tolerant is the amphidiploid *B.napus*, the trait having been likely from the A and C genomes.

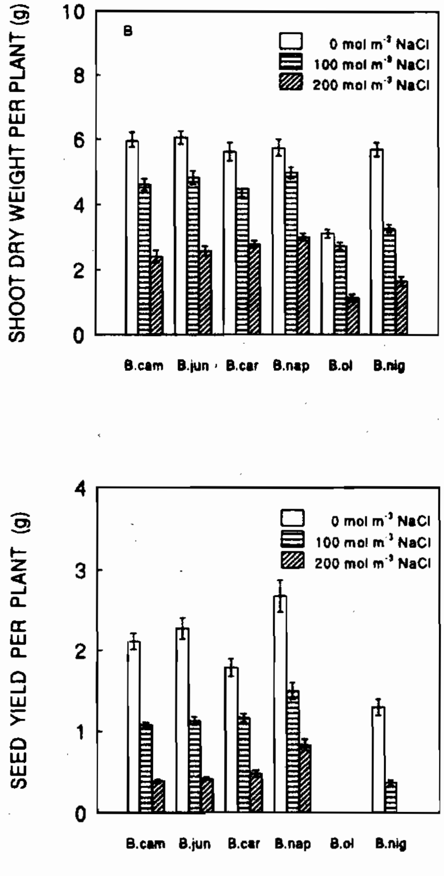


Figure 1. Shoot dry weights and seed yield per plant of six *Brassica* species grown in sand culture at 100 and 200 mol m^{-3} NaCl, plus control without NaCl (n=4). Figures in parentheses are percentage of control values.

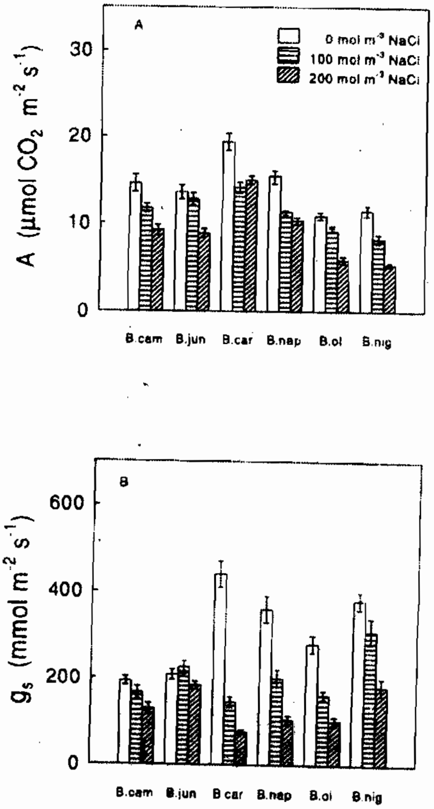


Figure 2. Assmilation rate (A) and stomatal conductance (g_s), of six *Brassica* species when 23 days old plants were exposed to varying concentrations of NaCl in sand culture for 28 days.

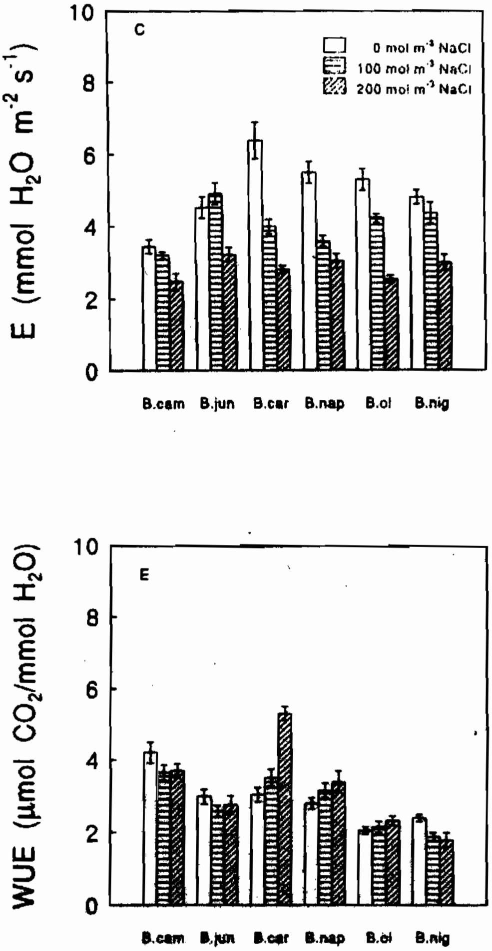


Figure 3. Transpiration rate (E) and water use efficiency (WUE) of six *Brassica* species when 23 days old plants were exposed to varying concentrations of NaCl in sand culture for 28 days.

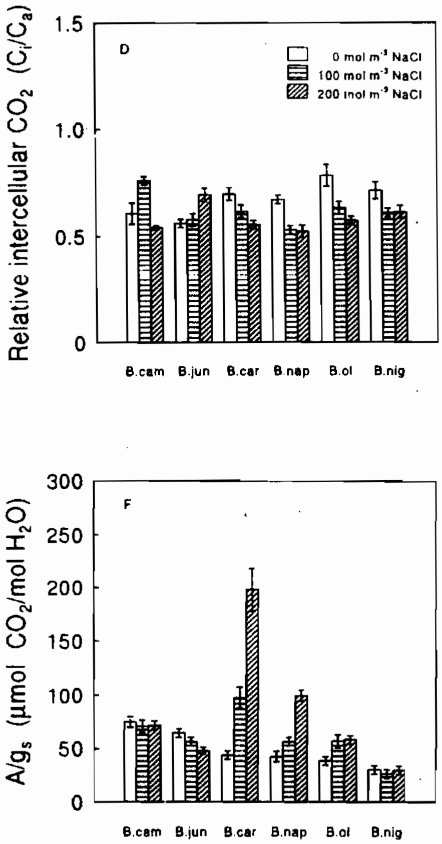


Figure 4. Relative intercellular CO_2 concentration (C_i/C_a) and intrinsic water use efficiency (A/g_s) of six *Brassica* species when 23 days old plants were exposed to varying concentrations of NaCl in sand culture for 28 days.

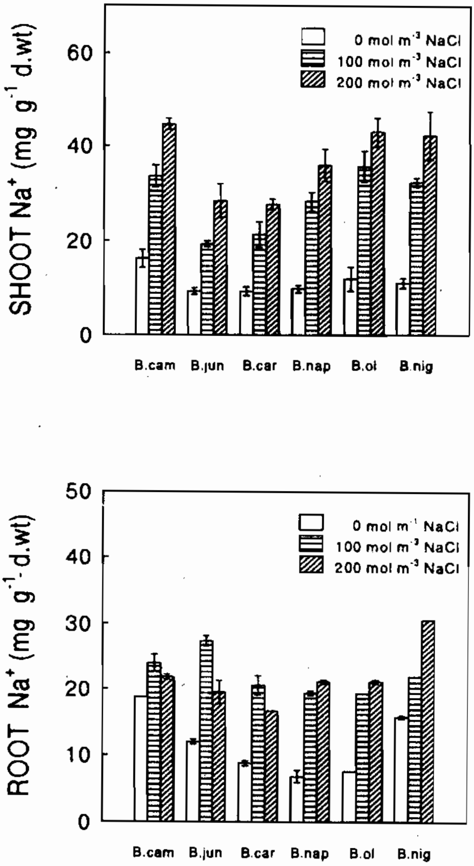
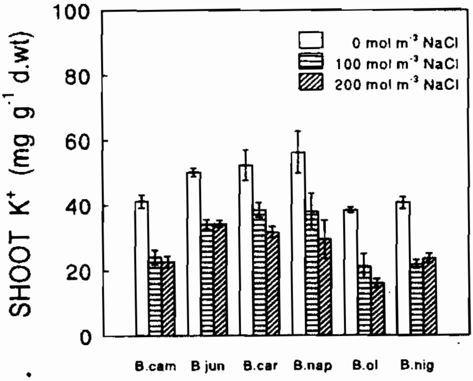


Figure 5. Concentration of Na^+ ion in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 200 mol m^{-3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).



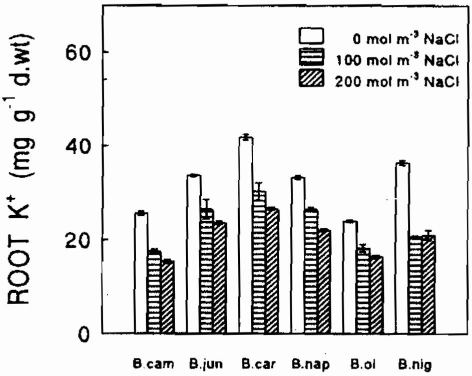
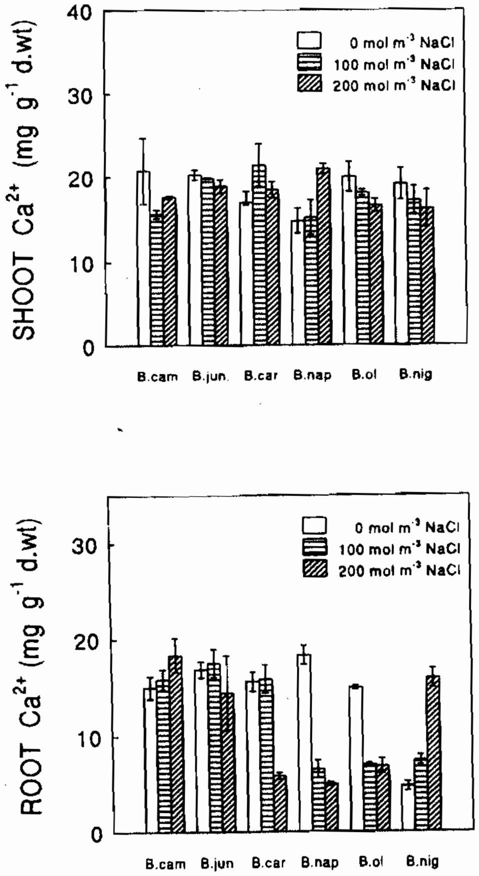


Figure 6. Concentration of K^+ ion in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 200 mol m^{-3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).



Figue 7. Concentration of Ca^+ ion in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 200 mol m^{-3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).

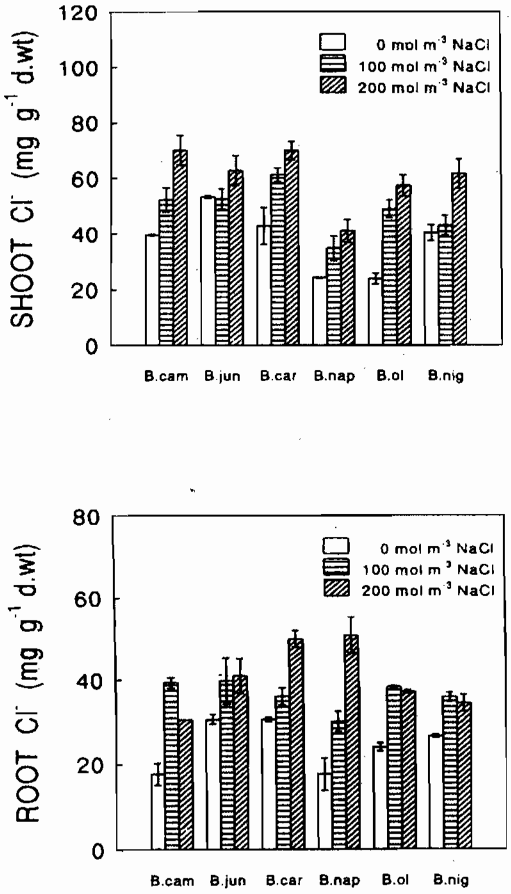


Figure 8. Concentration of Cl^- ion in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 200 mol m-^{3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).

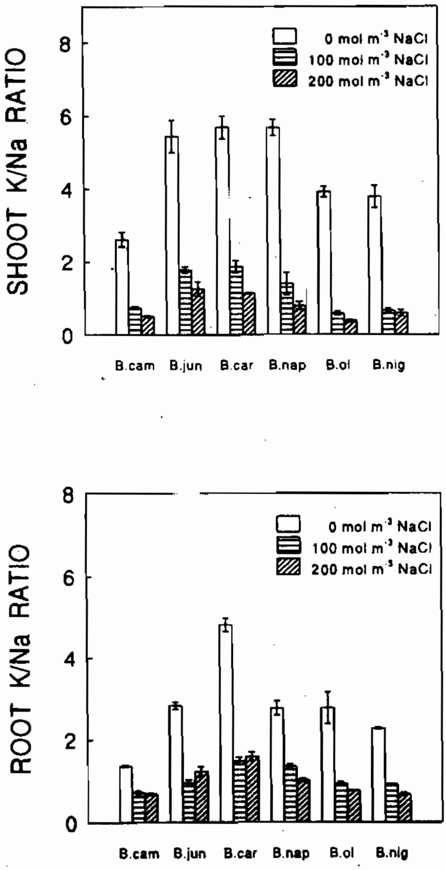


Figure 9. K/Na ratios in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 200 mol m^{-3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).

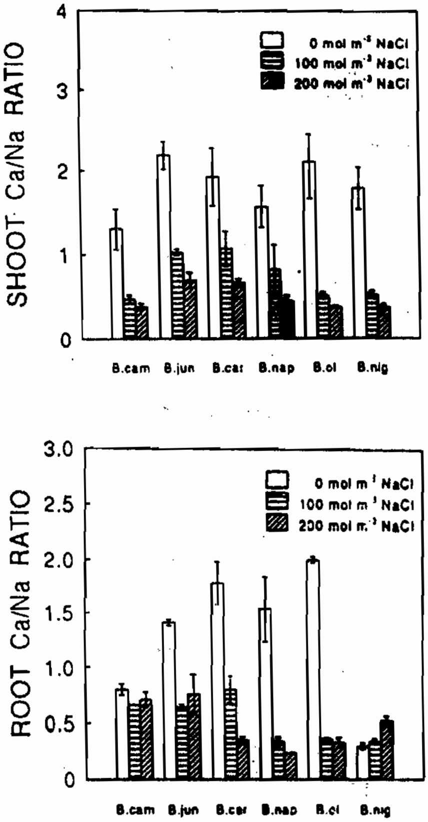


Figure 10. Ca/Na ratios in shoots and roots of six *Brassica* species when 23 days old plants were exposed to 100 and 2010 mol m^{-3} NaCl in sand culture for 28 days and control, with 0 NaCl (n=4).

References

Ashraf, M., 1994. Breeding for salinity tolerance in plants. *CRC Crit. Rev. Plant Sci.*, 13: 17-42.

Ashraf, M., T. McNeilly,., 1990. Responses of four *Brassica* species to sodium chloride. *Environ. Exp. Bot.*,30: 475-487.

Bowman, W.D., 1988. Ionic and water relations responses of two populations of a non-halophyte to salinity. *J. Exp. Bot.* 39: 97-105.

Carvajal, M., M. Martinez,., C.F. Alcaraz,. 1999. Physiological function of water channels as affected by salinity in roots of paprika pepper. *Physiol. Plant*, 105: 95-101.

Chandra Babu, R., P.S. Srivinisan,., N. Natarajaratnam, S.R. Rangasamy, 1985. Relationship between leaf photosynthesis and yield in blackgram (*Vign mungo* L. Hepper) genotypes. *Photosynthetica*, 19: 159-163.

Constable, G.A., H. M. Rawson, 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. *Aust. J. Plant Physiol.*, 7: 89-100.

Cornish, K., J.W. Radin., E.L Turcotte., Lu. Z. Zeiger. 1991. Enhanced photosynthesis and stomatal conductance of Pima cotton (*Gossypium barbadense* L.) bred for increased yield. *Plant Physiol.*, 97: 484-489.

Crosbie, T.M., R.B. Pearce. 1982. Effects of recurrent phenotypic selection for high and low photosynthesis on agronomic traits in two maize populations. *Crop Sci.*, 22: 809-813.

Downey, R.K. 1990. Brassica oilseed breeding – achievements and opportunities. *Plant Breed. Abstracts* 60: 1165-1170.

Dubey, R.S., 1997. *Photosynthesis in plants under stressful conditions*. In: Pessarakli, M. (ed.) Handbook of Photosythesis. Pp. 859-875. Marcel Dekker, New York.

Faville, M.J., W.B. Silvester., T.G. Green., W.A. Jermyn. 1999. Photosynthethic characteristics of three asparagus cultivars differing in yield. *Crop Sci.*, 39: 1070-1077.

Flowers, T.J., P.F., Troke. A.R., Yeo. 1977. The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.* , 28: 89-121.

Gorham, J., A. Britol., E.M. Young.., R.G. Jones.1991. The presence of the enhanced K/Na discrimination trait in diploid *Triticum* species. *Theor. Appl. Genet.*, 82: 729-736.

Greenway, H., R., Munns. 1980. Mechanism of salt tolerance in non-halophytes. *Annu. Rev. Plant Physiol.*, 31, 149-190.

Hawkins, H.J. and O.A.M. Lewis. 1993. Combintion effect of NaClsalinity, nitrogen form and calcium concentration on the growth andionic content and gaseous properties of *Triticum aestivum* L. cv. Gamtoos. *New Phytol.*, 124: 161-170.

He, T., Cramer, G.R., 1992. Growth and mineral nutrition of six rapid-cycling *Brassica* species in response to sea water salinity. *Plant Soil.* , 139: 285-294.

Hemingway, J.S., 1976. Mustards – *Brassica spp. and Sinapis alba* (Cruciferae). In: Simmonds, N.W. (ed.), Evolution of crop plants. pp. 56-59. Longman, London.

Kumar, D., 1995. Salt tolerance in oilseed Brassicas – present status and future prospects. *Plant Breed. Abstracts*, 65: 1438-1447.

Mäkela, P., Kontturi, M., Pehu, E., Somersalo, S., 1999. Photosynthetic response of drought- and salt-stressed tomato and turnip rape plants to foliar-applied glycinebetaine. *Physiol. Plant.*, 105: 45-50.

Malik, R.S., 1990. Prospects for *Brassica carinata* as an oilseed crop in India. *Exp. Agric.*, 26: 125-129.

McNaughton, I.H., 1976. *Turnip and relatives – Brassica campestris (Cruciferae)*. In: Simmonds, N.W. (ed.), Evolution of crop plants. Pp. 45-48. Longman, London.

Melesse, T., Caesar, K., 1992. Stomatal and non-stomatal effects of salinity on photosynthesis in faba beans (*Vicia faba* L.). J. Agron. Crop Sci., 168: 345-353.

Munshi, S.K., Bhatia, N., Dhillon, K.S., Sukhija, P.S., 1986. Effect of moisture and salt stress on oil filling in *Brassica* seeds. *Proc. Indian Natl. Sci. Acad.*, B52: 755-759.

Pettigrew, W.T., Meredith, W.R., 1994. Leaf gas exchange parameters vary among cotton genotypes. *Crop Sci.*, 34: 700-705.

Radin, J.W., Lu, Z.M., Percy, R.G., Zeiger, E., 1994. Genetic variation for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. *Proc. Natl. Acad. Sci.*, USA 91: 7217-7221.

Rana, R.S., Singh, K.N., Ahuja, P.S. 1980. *Chromosomal variations and plant tolerance to sodic and saline soils*. In: Proceedings of an International Symposium on Salt afffected Soils. Pp. 467-493. 18-21 February 1980. Central Soil Salinity Research Institute, Karnal, India.

Ranjith, S.A., Meinzer, F.C., 1997. Physiological correlates of variation in ntrogen-use efficiency in two contrasting sugarcane cutlivars. *Crop Sci.*, 37: 818-825.

Rawson, H.M., Constable, G.A., 1980. Carbon production of sunflower cultivars in field and controlled environments. I. Photosynthesis and transpiration of leaves, stems and heads. *Aust. J. Plant Physiol.*, 7: 555-573.

Rawson, H.M., Richards, R.A., Munns, R., 1988. An examination of selection criteria for salt tolerance in wheat, barley and triticale genotypes. *Aust. J. Agric. Res.*, 39: 759-772.

Robinson, S.P., Downton, W.J.S., Millhouse, J.A., 1983. Photosynthesis and ion content of leaves and isolated chloroplasts of salt-stressed spinach. *Plant Physiol.*, 73: 238-242.

Sage, R.F., R.W. Pearcy. 1987. The nitrogen use efficiency of C_3 and C_4 plants. II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). *Plant Physiol.*, 84: 959-963.

Seemann, J.R., C. Critchley.1985. Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt-sensitive species, *Phaseolus vulgaris* L. *Planta,* 164: 151-162.

Shah, S.H., J. Gorham., , B.P. Forster., R.G. Jones.1987. Salt tolerance in the Triticeae: the contribution of D genome to cation selectivity in wheat. *J. Exp. Bot.*, 36: 254-259.

Shannon, M.C., Grieve, C.M., 1999. Tolerance of vegetable crops to salinity. *Scientia Hort.*, 78: 5-38.

Stebbins, G.L., 1966. Chromosomal variations and evolution. *Science,* 152: 1463-1469.

Taiz, L., E. Zeiger.1998. *Plant physiology*. Second edition. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Wyn Jones, R.G., J. Gorham., E. McDonnell. 1984. *Organic and inorganic solute contents as selection criteria for salt tolerance in the Triticeae*. In: Staples, R. and Toennissen G.H. (eds.), Salinity tolerance in plants: Strategies for crop improvement. pp. 189-203. Wiley and Sons, New York.

Yeo, A.R.. 1998. Molecular biology of salt tolerance in the context of whole-plant physiology. *J. Exp. Bot.*, 49: 915-929. p