CHAPTER 8

GENERAL DISCUSSION

Due to the problem of salinity worldwide efforts are being made to combat it. One strategy in dealing with salinity has been suggested to be the growing of salt tolerant plants and this has increased the need to understand salt tolerance in plants. Amaranth adapts well to diverse environments, is relatively free from serious pests and diseases, is easy to cultivate and has high nutritive value. It is, therefore, a promising crop for arid and semi-arid areas. However, such areas suffer from salinity problems. Compared to many other crops, amaranth has received relatively little research attention regarding salinity effects. The approach of this study was to focus on some of the responses of amaranth genotypes to salinity in order to assess salt tolerance in this species.

8.1 Salinity tolerance at different stages of plant development

In a study evaluating the effect of salinity stress on amaranth seed germination and seedling growth (Chapter 2), it was found that salinity reduced seed germination and seedling growth. However, amaranth was more tolerant during germination than during emergence and seedling growth. These results are in agreement with reports on Lentil (*Lens culinaris* Medic.) (Ashraf and Waheed, 1990), *Hordeum* spp (Mano and Takeda, 1998) and *Phaseolus* species (Bayuelo-Jiménez *et al*., 2002). These authors also demonstrated that salinity tolerance varies with plant ontogeny. Furthermore, initiation of salinity at different growth stages after seedling emergence (Chapter 3) showed that salinity tolerance in amaranth differs with the growth stage at which salinity is initiated. Amaranth was more tolerant to salinity when it was initiated at the 4-leaf stage than at cotyledon stage. Epstein and Rains (1987) has reported that during plant growth, the form and function of various organs change and that the plant's ability to respond to the salt stress depends upon the genes that are functioning at the stage of development during which the stress occurs. The relative sensitivity could change from one developmental stage to another. One of the reasons for decreasing sensitivity with age could be a gradual acclimation of the crop to salinity.

Evidence collected from various species suggests that salt tolerance is a developmentally regulated stage-specific phenomenon, so that tolerance at one stage of development may not be correlated with tolerance at other developmental stages (Shannon, 1986). Therefore, specific stages throughout the ontogeny of the plant, such as germination and emergence, seedling survival and growth should be evaluated separately during the assessment of germplasm for salt tolerance. Such assessments may facilitate development of cultivars with salt-tolerance characteristics throughout the ontogeny of the plant.

Information on the growth stage response to salinity within a crop is important in adopting suitable genetic and management strategies for saline soils. For example, if a crop is more sensitive during one stage than another, there is an opportunity to regulate the salinity of irrigation water during the season to minimize salt injury at the sensitive stage. One way is to substitute fresh water for saline for the duration of the sensitive stage. This procedure has been reported to markedly increase the apparent salt tolerance of some crops such as maize (Pasternak *et al.,* 1985).

8.2 Genotypic variability

Various strategies have been adopted by plant scientists in overcoming salinity and one important component is the evaluation of genetic variability of the cultivated species or its wild relatives to identify a tolerant genotype that may sustain a reasonable yield on salt affected soils (Kingsbury and Epstein, 1984). Genotypic variation in salinity tolerance at the germination stage and later amaranth growth stage was reported in Chapter 2 and 3. It was demonstrated that *A. tricolor* and Accession ’83 were among the most salt tolerant genotypes during germination at 100 and 200 mM NaCl, but they were sensitive during emergence and early seedling growth. In Chapter 4, it was found that when amaranth plants were exposed to salinity one month after seeding *A. hypochondriacus* and *A. cruentus* were more tolerant than *A. tricolor* and Accession ’83. The latter two genotypes did not survive in 200 mM NaCl treatment and the reduction in dry mass due to lower levels of salinity was much higher than in the former two genotypes. Thus, selection of plants for salinity tolerance should not only be based on tolerance at seed germination since ultimately the final yield is the most important determinant factor for salinity tolerance.

Some of the strategies used by amaranth for salinity tolerance included efficient use of water and assimilate partitioning. *A. hypochodriacus* and *A. cruentus* utilized water more efficiently than *A. tricolor* and Accession '83, and this was related to lower stomatal conductance and reduced transpiration in the former genotypes. Although *A. tricolor* and Accession '83 had higher photosynthetic rates, dry mass was reduced to a greater extent than in *A. hypochondriacus* and *A. cruentus.* This shows that factors other than photosynthesis such as osmotic adjustment and protein synthesis may have contributed to plant growth (Wang and Nii, 2000). In plant production the marketable component of the plant is the most important. Under salinity stress *A. hypochondriacus* and *A. cruentus* partitioned most of the assimilates towards shoot growth and were able to maintain higher dry mass production than *A. tricolor* and Accession '83.

8.3 Salinity and water stress interactions

Salinity is normally associated with aridity, yet there is little or no information concerning the interactive effect of salinity and water stress in amaranth. This initiated the trials presented in Chapter 5. When amaranth plants were submitted to water stress, salt stress and a combination of water and salt stress, plants under salt stress and those in combined water and salt stress had higher biomass than those under water stress. This may have been due to a number of reasons:

a) Salt and salt + water stressed plants maintained higher water use efficiencies as a result of reduced stomatal conductance and transpiration rates compared to water stressed plants.

b) Increased salt concentration in the root medium or water stress led to an osmotic adjustment (lowering of leaf Ψ_π) that is generally accepted as an adaptation to salinity or water stress (Ghoulam *et al*., 2002; Iannucci *et al*., 2002). However, there was a greater adjustment in salt and salt + water stressed plants than in water stressed plants. According to Wyn Jones (1981) and Raven (1985), osmotic adjustment by salt accumulation, which may have occurred in salt and salt + water stressed plants, is less energy and carbon demanding than the adjustment by organic solutes that may have taken place in water stressed plants.

Furthermore, salt-treated plants and those submitted to salt + water stress were able to survive for a longer period before wilting because of the reduced growth rate of plants, thereby decreasing the rate at which soil water is depleted (Glen and Brown, 1998). This implies that in areas with erratic rainfall, plants irrigated with saline water of low EC may be able to survive the dry period before the next rain compared to those irrigated with high quality water.

8.4 Amelioration of salinity stress effects by Ca nutrition and seed priming

One possible approach to reduce the effect of salinity on plant productivity is through the addition of calcium supplements to irrigation water. Several reports have indicated that supplemental Ca^{2+} (usually up to at least 5 mM) may alleviate the reduced growth caused by NaCl salinity. The effect of Ca^{2+} in ameliorating salinity stress in amaranth was investigated in Chapter 6. Both $CaSO_4$ and $CaCl_2$ were effective in partly ameliorating salinity stress effects on photosynthesis, growth and mineral uptake. The positive effect of Ca^{2+} may be due to its role in the protection of cell membranes from the adverse effects of salinity (Busch, 1995). This topic deserves further research attention. The application of different Ca^{2+} concentrations in order to determine the optimum is required. Furthermore, it would be interesting to establish at what developmental stage application of supplemental Ca^{2+} is more effective, as well as the duration of application.

The effect of seed priming in salt tolerance in amaranth was investigated in Chapter 7. Seed priming improved seedling emergence, survival and growth. However, the greatest positive effect was from seeds primed with $CaSO_4$ + NaCl compared to those primed with the individual salts. This may have been partly due to improved salt adaptation from NaCl (Cayuela *et al*., 1996) combined with the protective effect from Ca^{2+} (Busch, 1995). In the trial reported in Chapter 7, seeds were imbibed for three hours and left to dry for two days before planting. Although there were positive effects of priming, it would be interesting to determine differences in the response with different periods of imbibition, as well as the time from priming to planting. On-farm field trials on the use of Ca^{2+} and seed priming for salinity stress amelioration will be necessary before final recommendations can be made.

8.5 Concluding remarks

This investigation evaluated some of the responses of amaranth to salinity stress and definite contributions were made:

1. Differences in salinity stress tolerance among amaranth genotypes were demonstrated and these differences varied with the stage of plant growth. Tolerance at one stage of development did not imply tolerance at another stage. Generally, amaranth was more salt tolerant at germination than at emergence and seedling growth, and more tolerant during the vegetative growth stage than at the cotyledon stage.
2. One of the responses to salinity stress involved changes in leaf anatomical features. This contributed to a better understanding of reasons for reduced photosynthetic rates with increasing salinity. In comparing two genotypes (*A. tricolor* and *A. cruentus*), it was found that although *A. tricolor* maintained relatively higher photosynthetic rates under saline conditions than *A. cruentus*, the reduction in growth was higher in the former genotype, showing that factors other than photosynthesis are involved in growth processes. There were negative correlations between leaf anatomical features (stomatal density, stomatal apertures and specific leaf area) and water use efficiency. From the results of this study, it may be concluded that *A. cruentus* may have attributed its salt tolerance to higher water use efficiency compared to *A. tricolor*.
3. It was demonstrated that salinity stress caused changes in the pattern of dry matter accumulation and partitioning to different plant parts of amaranth and genotype differences were observed. This may be one of the salt tolerance strategies.
4. The interactive effect of salinity and water stress was found to be less detrimental than the sum effects of the individual stresses. Hence, in drying soils, amaranth plants initially exposed to salinity stress may be able to survive longer than those supplied with high quality water under the same condition. Failure of photosynthesis to recover after the

removal of salt stress compared to water stress suggested that there was a toxic effect of salt concentration on the photosynthetic apparatus.

5. The capacity for supplementary calcium to ameliorate salinity stress effects on photosynthesis, growth and mineral uptake was demonstrated. One of the effects of calcium was found to be the reduction of Na^+ and Cl^- uptake.

6. The Priming experiment revealed that priming amaranth seed with NaCl, $CaSO_4$ or NaCl+$CaSO_4$ improved seedling emergence, survival and growth, and the positive effect of priming persisted to later plant growth. The priming effect of NaCl+$CaSO_4$ was higher than that of the other priming treatments.

8.6 Recommendations

- Further studies to determine the extent of variability for salt tolerance among other amaranth genotypes are greatly needed.
- A number of field studies are recommended since many physiological responses underlying adaptation may be overlooked when operating outside the field context.
- More information on the effect of salinization on productivity of land and the economic implications of the amelioration measures is necessary.