

Response of Amaranth to salinity stress

by

Elizabeth Nabwile Omami

Submitted in partial fulfillment of the requirements for the degree

Ph.D. Horticulture

In the Department of Plant Production and Soil Science

Faculty of Natural and Agricultural Sciences

University of Pretoria

March 2005

Supervisor: Prof. P. S. Hammes

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	i
DECLARATION	iii
LIST OF TABLES	iv
LIST OF FIGURES	viii
ABSTRACT	x
INTRODUCTION	1
CHAPTER 1	
LITERATURE REVIEW	5
1.1 Effects of salinity in agriculture – An overview	5
1.2 Causes of salinity	6
1.2.1 Primary cause	6
1.2.2 Secondary salinization	7
1.3 Salinity effects on plants	8
1.3.1 Effects of salinity on plant growth	10
1.3.2 Effects of salinity on water relations	10
1.3.3 Effect of salinity on leaf anatomy	11
1.3.4 Effect of salinity on photosynthesis	12
1.3.5 Effect of salinity on ion levels and nutrient contents	14
1.4 Salt tolerance	15
1.4.1 Interactions between salinity and environmental factors	16
1.4.2 Differences in salinity resistance among plant genotypes	16
1.4.3 Influence of growth stage on salinity resistance	17

1.5 Mechanisms of salt stress resistance	18
1.5.1 Selective accumulation or exclusion of ions	18
1.5.2 Synthesis of compatible solutes	19
1.5.3 Control of ion uptake by roots and transport into leaves	21
1.5.4 Changes in photosynthetic pathway under salinity	21
1.5.5 Induction of antioxidative enzymes by salinity	22
1.5.6 Induction of plant hormones by salinity	23
1.6 Managing salinity in agricultural production	24
1.6.1 Farm management practices	24
1.6.2 Amelioration through fertilization	25
1.6.3 Leaching	26
1.6.4 Uses of salt stress tolerant plants	26
1.7 The amaranth	27
1.7.1 Grain amaranth	27
1.7.2 Vegetable amaranth	28
1.7.3 Weedy species	29
1.7.4 Utilization and nutritional importance	29
1.7.5 Physiology	31
1.7.6 Salinity studies in amaranth	33

CHAPTER 2

EFFECT OF SALINITY STRESS ON AMARANTH SEED GERMINATION AND SEEDLING GROWTH

2.1 Abstract	35
2.2 Introduction	36
2.3 Materials and methods	37
2.3.1 Seed germination	37
2.3.2 Seedling emergence and growth	38
2.3.3 Statistical analysis	38

2.4 Results and discussion	39
2.4.1 Seed germination	39
2.4.2 Radicle elongation	48
2.4.3 Hypocotyl length	49
2.4.4 Effect of salinity on emergence of amaranth seedlings	51
2.4.5 Survival and growth of amaranth seedlings under salinity	54
2.5 Conclusion	58

CHAPTER 3

SALT TOLERANCE OF AMARANTH AS AFFECTED BY TIMING OF SALINITY STRESS INITIATION

3.1 Abstract	60
3.2 Introduction	61
3.3 Materials and methods	62
3.4 Results	64
3.4.1 Experiment 1	64
3.4.2 Experiment 2	70
3.5 Discussion	82
3.6 Conclusion	85

CHAPTER 4

DIFFERENCES IN SALINITY STRESS TOLERANCE IN TERMS OF GROWTH AND WATER USE EFFICIENCY AMONG FOUR AMARANTH GENOTYPES

4.1 Abstract	86
--------------	----

4.2 Introduction	87
4.3 Materials and methods	89
4.3.1 Plant culture	89
4.3.2 Salinity treatments	90
4.3.3 Gas exchange measurements	90
4.3.4 Water use	90
4.3.5 Plant growth measurements	91
4.3.6 Leaf anatomy	91
4.3.7 Statistical analysis	92
4.4 Results	92
4.4.1 Plant growth	92
4.4.2 Gas exchange	99
4.4.3 Transpiration and water use	101
4.4.4 Effect of salinity stress on leaf cell ultrastructure	103
4.5 Discussion	107
4.5.1 Plant growth	107
4.5.2 Transpiration and water use	109
4.5.3 Gas exchange	110
4.5.4 Leaf anatomy	112
4.6 Conclusions	113

CHAPTER 5

INTERACTIVE EFFECTS OF SALINITY AND WATER STRESS ON GROWTH, WATER RELATION AND GAS EXCHANGE IN AMARANTH

5.1 Abstract	115
5.2 Introduction	116
5.3 Materials and methods	118
5.3.1 Plant material and growth conditions	118
5.3.2 Water relations	119

5.3.3 Gas exchange	121
5.3.4 Water loss and water use efficiency	121
5.3.5 Statistical methods	121
5.4 Results	121
5.4.1 Plant growth	121
5.4.2 Water relations	125
5.4.3 Water loss and water use efficiency	128
5.4.4 Gas exchange	130
5.5 Discussion	132
5.5.1 Plant growth	132
5.5.2 Water relations	133
5.5.3 Water loss and water use efficiency	134
5.5.4 Gas exchange	136
5.6 Conclusion	137

CHAPTER 6

AMELIORATIVE EFFECTS OF CALCIUM ON MINERAL UPTAKE AND GROWTH OF SALT-STRESSED AMARANTH

6.1 Abstract	139
6.2 Introduction	140
6.3 Materials and methods	141
6.3.1 Plant material and culture	141
6.3.2 Plant growth measurements	142
6.3.3 Gas exchange	142
6.3.4 Relative water content	142
6.3.5 Electrolyte leakage	143
6.3.6 Chemical analysis	143
6.3.7 Statistical analysis	143
6.4 Results	144

6.4.1 Plant growth	144
6.4.2 Gas exchange	146
6.4.3 Relative water content	149
6.4.4 Membrane permeability	149
6.4.5 Ionic content	151
6.5 Discussion	154
6.5.1 Effect of calcium supplementation on vegetative growth of salt stressed amaranth	154
6.5.2 Effect of calcium supplementation on gas exchange of salt stressed amaranth	155
6.5.3 Effect of calcium supplementation on relative water content of salt stressed amaranth	156
6.5.4 Effect of calcium supplementation on membrane permeability of salt stressed amaranth	157
6.5.5 Effect of calcium supplementation on ion regulation of salt stressed amaranth	157
6.6 Conclusion	160

CHAPTER 7

SALT TOLERANCE OF AMARANTH AS AFFECTED BY SEED PRIMING

7.1 Abstract	162
7.2 Introduction	163
7.3 Materials and methods	164
7.3.1 Seed priming	165
7.3.2 Experiment 1	165
7.3.3 Experiment 2	166
7.4 Results	167
7.4.1 Experiment 1	167
7.4.1.1 Seedling emergence	167

7.4.1.2 Seedling survival	169
7.4.1.3 Seedling growth	172
7.4.2 Experiment 2	175
7.4.2.1 Photosynthetic rate	175
7.4.2.2 Relative water content	175
7.4.2.3 Plant growth	177
7.4.2.4 Ion content	180
7.5 Discussion	183
7.5.1 Experiment 1	183
7.5.1.1 Seedling emergence, survival and growth	183
7.5.2 Experiment 2	185
7.5.2.1 Photosynthetic rate and relative water content	185
7.5.2.2 Plant growth	186
7.5.2.3 Ionic content	187
7.6 Conclusions	188

CHAPTER 8

GENERAL DISCUSSION

8.1 Salinity tolerance at different stages of plant development	189
8.2 Genotypic variability	190
8.3 Salinity and water stress interactions	191
8.4 Amelioration of salinity stress by Ca nutrition and seed priming	192
8.5 Concluding remarks	193
8.6 Recommendations	194

REFERENCES	195
-------------------	------------

ACKNOWLEDGEMENTS

I am sincerely grateful to the Netherlands Organization for International Cooperation in Higher Education and Research (NUFFIC), Larenstein International Agricultural College (LIAC) and Moi University (Kenya) for providing funds of a cooperative project which enabled me pursue this study.

I am deeply indebted to Prof. P.S. Hammes for his able and tireless supervision, guidance, patience and helpful criticism throughout the study.

My gratitude also goes to the Vegetable and Ornamental Plant Institute, Agricultural Research Council, South Africa, for providing the seed used in this study, and to the technical and support staff at the University of Pretoria Experimental Farm for their assistance during the execution of experiments.

I thank Mr. C. Van der Merwe and Mr. A. Hall from the Microscopy and Microanalysis laboratory, Prof. Robbertse and R.W. Gilfillan, Department of Plant Production and Soil Science, University of Pretoria, for their assistance during the microscopy studies.

I am deeply grateful to my family members and especially to my husband Sammy Omami, my children: Andrew, Ken, Mike Linda and Brian for their unconditional love and encouragement and for being on my side. May God, surely continue to bless you.

I acknowledge the spiritual and moral support by Pastor Willy Booyesen and his wife Pastor Olga, brothers and sisters in Christ at the ELIM FULL GOSPEL CHURCH, BROOKLYN, PRETORIA as well as Pastor Morris Omondi and brethrens of REDEEMED GOSPEL CHURCH, ELDORET (KENYA) for their continued prayers.

To all my friends here in South Africa, especially to Mr. and Mrs. Kitheka, for opening their door to me at all times and making me feel at home away from home, Dankie and may you receive bountiful blessings.

Last but not least, I am so thankful to the Almighty God for His protection, guidance, provision and for seeing me through. Surely, His grace is sufficient and His promises are sure and AMEN. I give Him all the glory and honor.

DECLARATION

I, Elizabeth Nabwile Omami, hereby declare that this thesis for the degree Ph.D. in Horticulture at the University of Pretoria, South Africa, is my own work and has never been submitted at any other university.

Elizabeth Nabwile Omami

March 2005

LIST OF TABLES

	Page
CHAPTER 1	
Table 1.1 Classification of water	6
Table 1.2 Nutrient content of selected raw vegetable leaves	30
CHAPTER 2	
Table 2.1 Effect of NaCl and Na ₂ SO ₄ concentrations on radicle lengths of different amaranth genotypes	49
Table 2.2 Effect of NaCl or Na ₂ SO ₄ concentration on hypocotyl lengths of different amaranth genotypes	50
Table 2.3 Effect of NaCl and Na ₂ SO ₄ concentrations on seedling survival after 21 days in different amaranth genotypes	55
Table 2.4 Effect of genotype and Na ₂ SO ₄ concentration on seedling shoot fresh mass and lateral number of roots	57
CHAPTER 3	
Table 3.1 Effect of NaCl concentrations averaged across stage of salinity treatments application on plant vegetative growth of different amaranth genotypes	66
Table 3.2 Effect of stage of salinity treatment application averaged across NaCl concentrations on vegetative growth of different amaranth genotypes	68
Table 3.3 Effect of exposure to salinity for 14 days averaged across stage of salinity application on vegetative growth of different amaranth genotypes	72
Table 3.4 Effect of exposure to salinity for 14 days at different stages of growth averaged across NaCl concentrations on vegetative growth of different amaranth genotypes	73

Table 3.5	Effect of NaCl concentrations applied for 14 days at different stages of growth on photosynthetic rate of amaranth at the end of each stress period	77
------------------	---	----

Table 3.6	Effect of NaCl concentrations applied for 14 days at different stages of growth on stomatal conductance of amaranth at the end of each stress period	78
------------------	--	----

Table 3.7	Effect of NaCl concentrations applied for 14 days at different stages of growth on photosynthetic rate of amaranth after recovery from stress	80
------------------	---	----

Table 3.8	Effect of NaCl concentrations applied for 14 days at different stages of growth on stomatal conductance of amaranth after recovery from stress	81
------------------	--	----

CHAPTER 4

Table 4.1	Effect of NaCl concentrations in the nutrient solution on plant height, leaf number, leaf area and specific leaf area of four amaranth genotypes	95
------------------	--	----

Table 4.2	Effect of NaCl concentrations in the nutrient solution on total water loss by transpiration, transpiration rate and water use efficiency of different amaranth genotypes	102
------------------	--	-----

Table 4.3	Effect of NaCl concentrations in the nutrient solution on the number of stomata and length of stomatal aperture of two amaranth genotypes	103
------------------	---	-----

Table 4.4	Main effect of genotype and salinity stress on leaf tissue thickness of two amaranth genotypes	105
------------------	--	-----

CHAPTER 5

Table 5.1	Effect of water stress, salinity stress and salinity + water stress on leaf, stem and root dry mass and leaf area of <i>A. tricolor</i> and <i>A. cruentus</i>	123
------------------	--	-----

Table 5.2	Effect of water stress, salinity stress and salinity + water stress on transpiration and water use efficiency of <i>A. tricolor</i> and <i>A. cruentus</i>	129
------------------	--	-----

CHAPTER 6

Table 6.1	Effect of calcium supplementation on amaranth plant growth	144
------------------	--	-----

Table 6.2	Effect of calcium supplementation on leaf area of two amaranth genotypes	145
------------------	--	-----

Table 6.3	Effect of calcium supplementation on stomatal conductance of two amaranth genotypes	146
Table 6.4	Effect of calcium supplementation on photosynthetic rate of two amaranth genotypes	148
Table 6.5	Effect of calcium supplementation on relative water content of two amaranth genotypes	149
Table 6.6	Effect of calcium supplementation on electrolyte leakage in leaves of two amaranth genotypes	150
Table 6.7	Effect of calcium supplementation in salt stressed plants on the concentration of different ions in shoots and roots of two amaranth genotypes	152
Table 6.8	Effect of calcium supplementation on $\text{Ca}^{2+}/\text{Na}^{+}$ and $\text{K}^{+}/\text{Na}^{+}$ ratios of two salt stressed amaranth genotypes	153
Table 6.9	Effect of calcium supplementation on nitrogen and phosphorus content of two salt stressed amaranth	154
 CHAPTER 7		
Table 7.1	Effect of seed priming on the survival rates of seedlings of amaranth under salinity	173
Table 7.2	Main effects of genotype, NaCl salinity and seed priming on shoot and root length, shoot and root dry mass of amaranth	174
Table 7.3	Main effects of genotype, NaCl salinity and seed priming on photosynthetic rate of amaranth	176
Table 7.4	Main effects of genotype, NaCl salinity and seed priming on relative water content of amaranth	177
Table 7.5	Effects of seed priming on plant height, leaf number and leaf area of amaranth under salinity	178
Table 7.6	Interactive effect of NaCl salinity and genotype on amaranth plant height, leaf number and leaf area	179
Table 7.7	Main effects of genotype, NaCl salinity and seed priming on shoot and root dry mass and root:shoot ratio of amaranth	181

Table 7.8 Main effects of genotype, NaCl salinity and seed priming on ion content in leaves of amaranth	182
Table 7.9 Interactive effects of NaCl salinity and seed priming on Na ⁺ content, Ca ²⁺ :Na ⁺ and K ⁺ :Na ⁺ ratios of amaranth	183

LIST OF FIGURES

	Page
CHAPTER 1	
Figure 1.1 <i>Amaranthus cruentus</i> in flower	28
CHAPTER 2	
Figure 2.1 Effect of NaCl and Na ₂ SO ₄ on germination of amaranth genotypes	40
Figure 2.2a Effect of NaCl and Na ₂ SO ₄ concentration on the time course of germination of <i>A. tricolor</i> , Accession '83 and <i>A. dubius</i>	42
Figure 2.2b Effect of NaCl and Na ₂ SO ₄ concentration on the time course of germination of <i>A. hypochondriacus</i> , <i>A. cruentus</i> and <i>A. hybridus</i>	43
Figure 2.3 Effects of NaCl and Na ₂ SO ₄ concentrations on the germination rate of different amaranth genotypes	47
Figure 2.4 Effect of NaCl and Na ₂ SO ₄ concentrations on the seedling emergence of different amaranth genotypes	53
Figure 2.5 Effect of Na ₂ SO ₄ concentrations on root and shoot lengths of three amaranth genotypes	56
CHAPTER 3	
Figure 3.1 Effect of NaCl concentrations and stage of application on relative shoot dry mass of different amaranth genotypes	69
Figure 3.2 Effect of NaCl concentrations applied for 14 days at different stages of growth on relative shoot dry mass of different amaranth genotypes	75
CHAPTER 4	
Figure 4.1a & b <i>A. tricolor</i> and <i>A. cruentus</i> plants salinized with 0, 25, 50, 100 and 200 mM NaCl solutions	93
Figure 4.2 Effect of NaCl concentrations in the rooting medium on shoot and root dry mass of amaranth genotypes	96

Figure 4.3 Effect of NaCl concentrations in nutrient solution on dry mass partitioning among root, stem and leaf of different amaranth genotypes	98
Figure 4.4 Effect of increasing NaCl concentrations in the growth medium on stomatal conductance and photosynthetic rate of four amaranth genotypes	100
Figure 4.5 Scanning electron micrographs showing stomates and cell size on upper leaf surface of amaranth	104
Figure 4.6 Leaf cross sections of control and salt-treated amaranth showing different tissue thicknesses	106
 CHAPTER 5	
Figure 5.1 Growth of <i>A. cruentus</i> and <i>A. tricolor</i> as affected by iso-osmotic water and salt stresses	124
Figure 5.2 Leaf water potential, osmotic potential and turgor potential of <i>A. tricolor</i> and <i>A. cruentus</i> exposed to iso-osmotic stress treatments	126
Figure 5.3 Effect of water stress, salt stress and combined water and salt stress on relative water content of <i>A. tricolor</i> and <i>A. cruentus</i>	128
Figure 5.4 Effect of water stress, salt stress and combined water and salt stress on stomatal conductance and photosynthetic rate of <i>A. tricolor</i> and <i>A. cruentus</i>	131
 CHAPTER 6	
Figure 6.1 Growth of <i>A. tricolor</i> and <i>A. cruentus</i> in saline medium and supplemental calcium	147
 CHAPTER 7	
Figure 7.1 Effect of NaCl concentration on emergence of amaranth seedlings derived from non-primed and primed seeds	168
Figure 7.2 Effect of NaCl concentration on time course of emergence of primed and non-primed seeds of <i>A. tricolor</i>	170
Figure 7.3 Effect of NaCl concentration on time course of emergence of primed and non-primed seeds of <i>A. cruentus</i>	171

Responses of Amaranth to salinity stress

by

Elizabeth Nabwile Omami

Supervisor: Prof. P. S. Hammes

Department: Plant Production and Soil Science

Degree: Ph.D.

ABSTRACT

Salinity continues to be one of the world's most serious environmental problems in agriculture. The increasing world population and urbanization are forcing farmers to utilize marginal lands as well as poor quality water. One of the strategies in dealing with salinity is growing salt tolerant plants and there has been increased need to understand the effects of salinity on crops. Owing to its high nutritive value and wide adaptability to diverse environments, amaranth is considered a promising crop for marginal lands and semiarid regions. The objective of the study was to investigate the response of amaranth to salinity stress and evaluate stress amelioration by calcium and seed priming.

Salinity tolerance during germination and early seedling growth was examined for six genotypes of amaranth (*Amaranthus* species) at different salt concentrations ranging from 0 to 200 mM NaCl or Na₂SO₄. Enhancement of germination was observed at 25 mM, while increasing salt concentrations reduced the germination percentage as well as germination rate. *A.tricolor* and Accession '83 were able to germinate in 200 mM NaCl while there was no germination at 200 mM Na₂SO₄ in all the genotypes. Overall, Accession '83 was the most resistant and *A. hybridus* the most sensitive genotype, particularly at high salt concentrations. Inhibition of germination was greater in Na₂SO₄

than in NaCl salinity treatments. Amaranth was more salt tolerant at germination than at seedling growth. Seedling emergence, survival and growth were reduced by salinity and at much lower concentrations than at seed germination. Differences in salt tolerance were noted among the genotypes.

Salinity stress was initiated at different growth stages (cotyledon stage, 2-leaf stage and 4-leaf stage) in order to determine whether tolerance of amaranth differs with the stage of development. The treatment either continued until termination of the experiment or for 14 days at each stage. Amaranth plants were less sensitive to salinity when the stress was initiated at the 4-leaf stage. Lower salt concentrations had less detrimental effects than higher concentrations when applied at the cotyledon stage. Application of low salt concentration at cotyledon stage for 14 days did not have any effect on plant growth. The results indicate that it is feasible to use saline water for growing amaranth with minimum yield losses if salt concentration, duration of exposure and time of salinization are carefully managed.

Differences in salinity tolerance among amaranth genotypes were analyzed in terms of plant survival, growth, gas exchange, water use and leaf anatomical changes. *A. hypochondriacus* and *A. cruentus* showed greater tolerance to salinity since they survived in 200 mM NaCl treatment and the reduction in growth at 50 and 100 mM was lower than that of *A. tricolor* and Accession '83. *A. hypochondriacus* and *A. cruentus* were more efficient water users and partitioned photosynthates towards shoot growth as opposed to the other two genotypes. Photosynthetic rate, stomatal conductance, stomatal density and apertures were reduced by salinity but were higher in *A. tricolor* than in *A. cruentus*. Salinity resulted in *A. cruentus* developing thicker leaves compared to *A. tricolor*. Productivity on saline soils can be increased by growing genotypes more tolerant to salinity.

The interactive effect of salinity and water stress on amaranth plant growth was evaluated. It was found that the reduction in shoot growth was greater in plants submitted

to water stress than in those submitted to salt or salt + water stress. Water use efficiency was increased while leaf water and osmotic potentials were reduced by the salinity stress treatments. In drying soil plants previously salinized had a greater degree of osmotic adjustment, so that plants were able to continue growth for a longer period compared to water stressed plants.

The effect of calcium in ameliorating salt stress was investigated. Supplementary calcium, either as CaSO_4 or CaCl_2 ameliorated the negative effects of salinity on growth, gas exchange, membrane permeability and mineral uptake. In a separate experiment it was shown that it is feasible to mitigate the adverse effects of salinity on amaranth seed germination, seedling survival and growth by seed priming and that the positive effect of priming persisted to vegetative growth stage. Priming with $\text{CaSO}_4 + \text{NaCl}$ showed a greater positive response than priming with the individual salts.

Key words: *Amaranthus*, calcium, gas exchange, germination, growth, membrane permeability, photosynthesis, salinity stress, salt tolerance, seed priming, water relations, water stress, water use efficiency (WUE).

INTRODUCTION

Salinity is one of the world's most serious environmental problems in agriculture. It is estimated that about one-third of the world's cultivated land is affected by salinity (Perez-Alfocea *et al.*, 1996). The National Academy of Sciences of the USA includes salinization of soils and waters as one of the leading processes contributing to a possible worldwide catastrophe (Francois and Maas, 1994). The increasing world population, especially in arid and semi-arid regions, food shortages, and land scarcity are compelling the use of lands not utilized because of salinity and other soil stresses. Salinity and sodicity problems are characterized by an excess of inorganic salts and are common in the arid and semi-arid lands (ASAL) where they have been naturally formed under the prevailing climatic conditions and due to the high rates of evapotranspiration and lack of leaching water (Mengel and Kirkby, 1982; Shannon *et al.*, 1994). In the arid and semi-arid parts of Africa, for instance, salinity and alkalinity are major problems affecting about 24% of the continent (Reich *et al.*, 2004). According to Eswaran *et al.* (1997) about 30% of the population of Africa or about 250 million people are living on or are dependent on this type of land.

Although more frequent in arid lands, salt-affected soils are also present in areas where salinity is caused by poor quality of irrigation water and increases markedly during the dry season (De Pascale *et al.*, 1997; Sifola and Postiglione, 2002). As competition for fresh water increases due to increasing population, water of better quality is used primarily for domestic purposes, whereas water of lower quality e.g. saline or polluted water (drainage water generated by irrigation agriculture, marginal-quality waters generated by municipalities) often is used for irrigation (Khroda, 1996; Oster, 2000; Bouwer, 2002). Wanjogu *et al.* (2001) reported that land degradation by salinization is on the increase where the use of poor quality irrigation water is a common practice in arid and semi-arid lands. However, there seems to be a general lack of information on the prevalence and composition of saline aquifers in sub-Saharan Africa (Karlberg and Penning de Vries, 2003). Although some countries, such as South Africa, Botswana and

Zimbabwe have documented the presence of saline aquifers, Karlberg and Penning de Vries (2003) reiterated that information as to what extent saline water is being used for irrigation in sub-Saharan Africa is lacking.

From the perspective of plant productivity, salinity problems accentuate year after year as a result of repeated irrigation with poor quality water. The concentration of salt in the soil rises due to evaporation. Similarly, the salt concentration in plant tissues increases as water is lost through the process of transpiration. Salt problems unrelated to irrigation are also known. Excessive fertilizer application, susceptible soil types, and drought can combine to play a major role in accentuating the toxic effect of salts on crop yield (Parker *et al.*, 1983).

Agricultural production in arid and semiarid regions of the world, which depends on irrigation, faces a serious challenge because it must increase or at least maintain crop productivity while coping with ever more saline irrigation water. Irrigation with saline water is successfully practiced in many countries such as Israel, Italy and the US (Rhoades *et al.*, 1992). The success of using such water is dependent on advances in the knowledge of the many factors involved in plant salt tolerance.

Salt accumulation in soils induces physiological and metabolic disturbances in crops affecting development, growth, yield and quality of crops (Pardossi *et al.*, 1999; Mavrogianopoulos *et al.*, 1999; del Amor *et al.*, 2000; Mer *et al.*, 2000; Silveira *et al.*, 2001). Reduction in growth results from salinity effects on dry matter allocation, ion relations, water status, biochemical reactions or a combination of many physiological factors. However, the severity of salt damage has been found to be dependent on the meteorological conditions, soil type (Shannon *et al.*, 1994), species and cultivar (Rhoades *et al.*, 1992; Vicente *et al.*, 2004), growth stages of the plant (Yeo *et al.*, 1991; Botia *et al.*, 1998; Carvajal *et al.*, 1998), time interval between irrigations, amount of water distributed and time of exposure to saline water (Oster, 1994). Such variability suggests that environment and species-specific assessments of plant salt tolerance are both required in order to obtain conclusive information regarding the cultivation of a certain

species using saline water of specific concentration. This is due to the fact that general guidelines for agricultural management may not respond to the species and/or environment-specific crop requirements for optimum production (Rhoades *et al.*, 1992; Dalton *et al.*, 2000).

The degree of salt stress on a plant depends on three responses:

- Shoot dehydration through the low water potential caused by osmotic stress (Dubey, 1997; Carvajal *et al.*, 1999);
- Nutritional imbalances caused by the interference of saline ions with essential nutrients in both uptake and translocation processes or partitioning within the plant (Liu and Zhu, 1998; Grattan and Grieve, 1999);
- Specific ion toxicity due to the accumulation of ions, particularly Na⁺ and Cl⁻ in the cytoplasm (Greenway and Munns, 1980; Yeo, 1998; Wahome *et al.*, 2001).

These three effects often coexist in soils exposed to salinization, and can persist throughout the growth season (De Pascale *et al.*, 2003a, b).

Sustained and profitable production of crops on salt-affected soil is possible if appropriate on-farm management practices are carried out. To be successful, growers require an understanding of how plants respond to salinity, the relative tolerances of different crops and their sensitivity at different stages of growth, and how different environmental conditions affect salt-stressed plants. A widespread practice to reduce the salt content in soils is leaching. However, with the rising cost of water, this may not continue to be a feasible method for the future. Increasing salinity has increased the need to understand the effects of salinity on crops, and genetic improvement of salt tolerance has become an urgent need for the future of agriculture in arid and semi-arid regions (Shannon, 1984; Owens, 2001). Breeding of salt tolerant crop varieties will require a clear understanding of plant response to salinity and the complex mechanisms of salt stress tolerance (Zhu, 2001; Apse and Blumwald, 2002).

As the problems of salinity become more severe Aronson (1985) and NRC (1990) have proposed the growing of alternative plants and crops suited to moderately saline conditions with the option of introducing under-exploited, salt-tolerant minor crops. Salt tolerant plants may provide a logical alternative for many developing countries.

Amaranth is used for its grain and is also consumed as a cooked vegetable in many parts of the world. Owing to its high nutritive value and a wide adaptability to diverse environments, amaranth has been considered a promising crop for marginal lands and semiarid regions (Cunningham *et al.*, 1992; Allemann *et al.*, 1996). The prospects for future cultivation of salt-tolerant, high-yielding genotypes of amaranth are very encouraging. However, despite a substantial amount of literature on responses of plants to salinity stress, little information is available on amaranth. The general objectives of this study were to better understand the response of amaranth to salinity stress by investigating:

- Differences in salinity tolerance in different amaranth genotypes at seed germination and vegetative growth stages.
- Salt tolerance of amaranth as affected by salt concentration and timing of salinity imposition after seedling emergence.
- Morphological and physiological traits that contribute to salinity tolerance in amaranth.
- Interactive effects of salinity and drought stress on amaranth growth and development.
- The ameliorative effects of calcium nutrition and seed priming on growth, mineral uptake and photosynthesis of salt-stressed amaranth.