INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
1560–8530/2001/03–2–250–255
http://www.ijab.org

Review
Stress Tolerance in Crop Plants

ASIF ALI KHAN, THOMAS MCNEILLY† AND F.M. AZHAR
Department of Plant Breeding and Genetics, University of Agriculture Faisalabad–38040, Pakistan
†School of Biological Sciences, The University of Liverpool, LIVERPOOL. L69 3BX UK

ABSTRACT

The presence of salts of different kinds in saline soils, and aluminium, zinc, manganese and copper in acid soils develop stressful conditions for plants, and result in poor yields of different crops. Therefore strategies have to be developed to make the plants adaptable to the unconducive environments. Better management practices could be used successfully for raising crops in the areas affected. Adaptation of some species to high salt concentrations provides evidence of the genetic potential existed in plants to cope with the unfavourable conditions. Variation, both between and within the species, and even at intra-varietal level does exist in different crops. Development of tomato, rice and barley varieties tolerant to salinity, and of maize tolerant to acidic-soils are the elegant examples in the domain of plant breeding. The studies on the genetic basis of tolerance in plants for salinity and toxicity due to aluminium, manganese, copper and zinc revealed that variation in tolerance was genetically controlled and thus heritable in nature. Thus, further improvement in tolerance to salinity and acidity may be possible utilising genetic resources available to researchers. Strong selection pressures may be used in order to identify tolerant individuals either from heterogeneous or segregating populations. Physiological mechanisms involved in controlling the responses to stress may aid in selecting successful plants. Therefore, an understanding of appropriate physiological mechanisms controlling stress tolerance is essential. Molecular analysis of genome at the DNA level is an additional tool for the breeders, and allows them to transfer and combine desirable genes with greater precision for greater benefits. The DNA marker technology is now being incorporated in breeding programmes, which has the potential to facilitate the selection for complex traits in early generations.

Key Words: Salinity tolerance; Aluminium tolerance; Manganese tolerance; Genetic variability

INTRODUCTION

The term stress is derived from the Latin word *stringere*, which means a constraining or impelling force. From crop production point of view, Grime (1979) defined stress as “the external constraints which limit the rate of dry matter production of all or part of the vegetation below its genetic potential”. However, Jones and Jones (1989) used economic yield, rather than dry matter production, to measure the response of plants to stress.

After planting a seed in soil, development and productivity of plant is subjected to numerous environmental stresses. Generally, plants are considered to be under stress when they experience a relatively severe shortage of an essential constituent or an excess of potentially toxic or damaging substance, and the plants usually face both the situations simultaneously. These abiotic soil stresses constitute a major limiting factor, which hamper plant productivity throughout the world (Clark & Duncan, 1993). Therefore strategies have to be developed to make use of these resources for food production. The present paper reviews the responses of plants to soil salinity, toxicity due to accumulation of aluminium and manganese, and other matters in soils. In addition, the genetic, physiological, and molecular basis of variation in responses to stresses have also been reviewed.

Evolution of stress tolerance. The evolutionary changes in plant populations are to be expected, rather inevitably, in any situation where stress is occurring consistently (Bradshaw & Hardwick, 1989). Stress as a constraint and stimulant, apart from affecting the individual, also promotes the development of better adapted genotypes. Several plant species are known to have evolved on contaminated soils, and thus developed the potential to grow successfully on affected soils, where non-tolerant individuals of the same species showed complete death (Bradshaw & McNeilly, 1981). This tolerance is specific to the individual metal, and is highly heritable (Gartside & McNeilly, 1974a,b). Similarly, there is ample evidence that salinity and drought tolerance in plants have also evolved in coastal areas and deserts, and obviously is the product of natural selection, and thus these species can be grown in saline environments. Such evidences on the evolution of stress tolerance suggest that possibility for improving stress tolerance in crop cultivars through selection and breeding does exist. This biological approach of tailoring the plants through selection and genetic means has received considerable attention these days, and a few varieties of different crops with enhanced tolerance have been developed and grown successfully under saline and acid soil conditions.

Soil salinity. The chemical and physical properties of air, soil and nutrients act, in most cases, in a multifactorial way, and in arid and semi-arid zones this phenomenon is most obvious in the development of the problem of soil salinity. Concurrently there is an increasing demand for new agricultural land in developing countries to feed their rapidly growing populations. Hence there is an urgent need to combat the effects of progressive loss of soil to agriculture through salinisation.

Soil salinity may be assessed by measuring total amount of exchangeable cations that a soil can retain, designated as the cation exchange capacity. The soluble cations which give saline soils their characteristics include Na^+, K^+, Ca^{2+}, Mg^{2+}, and Cl^-, SO_4^{2-}, NO_3^-, and HCO_3^- are the predominant anions (Tanji, 1990). Of these, chlorides, sulphates, and bicarbonates of sodium, calcium, and magnesium are of frequent occurrence in saline soils and irrigation water. Saline soils have an electrical conductivity (EC) of more than 4 dS m^{-1} in at least some part of the soil profile within 25 cm of the surface; exchangeable sodium percentage (ESP)< 15, pH < 8.5. According to the presence and concentrations of cations and anions, electrical conductivity, and exchangeable sodium percentage, the US Salinity Laboratory Staff (1954) has classified salt-affected soils as, saline (EC > 4 dS m^{-1}, ESP < 15), saline sodic (EC > 4 dS m^{-1}, ESP >15), and non-saline sodic soils (EC < 4 dS m^{-1}, ESP > 15).

The extent and distribution of saline soils. It is an unfortunate fact that agriculture in those parts of the world which mainly rely or have relied in the past upon canal irrigation are confronted with the serious challenge of increasing concentration of salts on their agricultural lands (Epstein *et al*., 1980). Due to rapid expansion of salination, a substantial portion of formerly arable lands is being converted to salt deserts every year. According to the estimates of FAO/UNESCO, 357.3 m ha in Australia, 211.7 m ha in North and Central Asia, 129.2 m ha in South America, 87.6 m ha in South Asia, 80.5 m ha Africa, 50.8 m ha in Europe, 20.0 m ha in Southeast Asia, 15.7 m ha in North America, and 2.0 m ha in Mexico and Central America had been affected by salinity (Szabolcs, 1993). On global basis a total of about 950 x 10^6 ha of land is affected by the spread of salts of different kinds (Flowers & Yeo, 1995). There is, however, a great variation in the distribution of salts near the root zone. The soils of Pakistan provide the best illustration of the advance of salination. It is claimed that, about 10 out of 15 m ha of potentially agricultural land had been affected to varying degrees by salinity and alkalinity with a rate of annual loss being some 40 x 10^3 ha (Wyn Jones, 1981).

Salination of irrigated lands. Canal irrigation plays a crucial role in agricultural productivity, and the need for more irrigation water is becoming inevitable in arid and semi-arid areas of the world. The problem of salination is increasing in areas commanded by canal irrigation, because most of the water in the hydrosphere is saline. Thus, availability of non-saline water for irrigation is becoming difficult. According to the estimates of FAO and UNESCO, 50% of irrigation schemes are salt-affected, and about 10 m ha of irrigated land of the world are thought to have gone out of cultivation each year due to secondary salination (Szabolcs, 1987). In India, 18-53% of the productive irrigated area has become water logged, and 11-38% is saline due to the running of 18 irrigation projects (Singh, 1992). It is reported that half of the total irrigated land in the world, 263 x 10^6 ha (FAO, 1998), has become salt-affected. From rapid population growth and increased dependence on irrigation for agricultural production in the developing countries of Asia, Africa and Latin America it appears that salination of agricultural land will become a life threatening problem in these parts of the world (Flowers & Yeo, 1995).

Acidic soils. Salinity is predominantly an environmental constraint to crop production in arid and semi-arid areas, while acidic soils characterised by low pH and excess of aluminium and manganese, also hamper crop production in tropical and sub tropical areas (Zeigler *et al.,* 1995).

Acidic soils, pH below 5.0, are reported to occur throughout the world, with the largest areas in tropical and sub-tropical regions. Except for extreme situations, pH *per se* rarely has a direct effect on plant growth. At very low pH, however, concentration of hydrogen ions may hinder, or even reverse cation uptake by plant roots (Foy *et al.,* 1988). The poor fertility of acid soils is mainly due to high levels of aluminium and/or manganese toxicity. The problems confronted by plants due to these toxicities are basically of two types. Firstly, the problem arises either as a consequence of nature of the parental material from which a particular soil was derived, or from the processes of soil formation, and secondly the problem of toxicity is anthropogenic in origin, having been imposed on soils by pollution originating from increasing growth of industrial and domestic impacts of humans on their environment (McNeilly, 1994).

The extent and distribution of acidic soils. On a global scale there are two main geographical belts of acidic soils: the humid northern temperate zone, and the humid tropics. The largest pool of potentially arable acid soils exists in the humid tropics, and comprise about 60% of the acid soils of the world (von Uexkull & Mutert, 1995). These authors quoted FAO estimates that acid soils cover about 30% of the total ice-free land or about 3950 x 10^6 ha of earth's surface. Of the total acid-soil area, 40.9% occurs in the Americas, 26.4% in Asia, 16.7% in Africa, 9.9% in Europe, and 6.1% in Australia and New Zealand. About 67% of the acid-soil area is under forests, 18% under savannas and prairie vegetation, 4.5% under arable crops, and less than 1% under perennial tropical crops. These soils comprise approximately 1.455 billion ha or roughly half of the non-irrigated arable lands in the world, and as such, are a major constraint to the world's agriculture production. Acidification of intensively cropped soils due to acid forming fertilisers is a serious problem in many parts of the world, notably in the USA (Jackson & Reisenauer, 1984) and the former USSR (Breburda, 1990).

Aluminium toxicity. Aluminium toxicity is the most important factor limiting plant growth in acidic soils throughout the world (Wright *et al.,* 1989), occurring almost exclusively on acidic soils below pH 5.0, (Woolhouse, 1983), but it has been reported to occur as high as pH 5.5 in some soils (Foy, 1974). This metal comprises approximately 7.5% by weight of the Earth's crust (Haug, 1984). The acidic soil have developed mainly through nitrification of ammonium ions as a result of sustained use of acid forming fertilisers, (McNeilly, 1994). Aluminium in non-acidic soils having pH > 5 is predominantly bound as insoluble oxide and complex aluminosilicates. However, as the soil pH decreases there is a release of ionic Al^{3+} and a reduction in the availability of exchangeable cations such as Ca^{2+}, Mg^{2+}, and K^+, and ionic aluminium become toxic to plants at micromolar concentrations (Parker *et al.,* 1989).

Manganese toxicity. Manganese is the second important toxic element in acidic soils, and is found in acidic soils of Africa and parts of Asia (Foy *et al.,* 1988). Manganese in divalent form (Mn^{2+}) is toxic to plant growth, and at low soil pH, MnO_2 is reduced to this toxic species of manganese. Manganese toxicity generally occurs in soil with pH of 5.5 or below, provided the soil contains sufficient amount of manganese. However, it can also occur in soils having higher pH, in poorly drained or compacted soils where reducing conditions favour the production of divalent manganese which plants may absorb.

Crop production on problem soils. Development and adoption of management methods/practices is also an important aspect of crop science for getting higher crop yields. Several reclamation and preventive measures were adopted to recover salt-affected areas. The most successful and commonly followed procedures to reduce the concentrations of salts include the use of good quality water and land management practices. The use of controlled irrigation with acceptable quality water and leaching of salts deep into the soil-profiles using large volumes of water tend to reduce the salt load in the soil. The use of chemicals such as gypsum, which is known to accelerate the movement of salts and water in the soil, has also been recommended for this purpose. Although these practices certainly have the potential to lessen the detrimental effects of salts in the root zone, due to non-availability of good quality water for irrigation and poor drainage in arid and semi-arid areas, adoption of these recommendations appears not to be a practical approach. A further development, "the engineering approach" aims to install efficient drainage system, and installation of tubewells has also been effective in alleviating the deleterious effects of soil salinity on plants. Although this physical approach has proved to be successful in reclaiming salty deserts, due to escalating cost of labour and energy the continued running of these projects does not appear economically feasible for developing countries (Shannon, 1984). Clearly in situations where it is not possible to modify the environment to suit the plant, plant breeders and geneticists are seeking to modify the plant to suit adverse soil conditions while maintaining reasonable and reliable yields. This alternative strategy, christened " the biological fix" has been increasingly emphasised as a possible alternative means to utilise under-exploited saline areas (Epstein *et al.,* 1980; Shannon, 1984). This approach constitutes genetic modifications of conventional crop plants through selection to improve their adaptation to salt stressed conditions.

In contrast to salinity, soils affected by deposition of aluminium and manganese in the root zone cannot be amended using soil amendments. Although application of lime can reduce the toxic effects of aluminium and manganese in the acid soils by increasing their soil pH, the application of lime is not universally possible due to non-availability of abundant supplies of lime to reclaim huge acreage. Moreover, liming the soil surface does little to correct chemical impediments in sub-soil root penetration, and thus has to be repeated. Therefore the best way of utilising these wasteland is through growing plant species which can survive under these toxic conditions.

Potential for breeding crops for stress tolerance. From evolutionary viewpoint, whether it may be occurring under natural conditions or through artificial means the availability of two components is essential. Firstly, there must be variation present in the breeding population, and secondly, the variation must be controlled by a significant genetic component.

There is sufficient knowledge about inter-generic differences in salt tolerance in different crops (Shalhevet &

Yaron, 1973; Shalhevet *et al.,* 1976). From these and later studies it has become clear that crop species differ widely in their potential for selection and breeding for enhanced salt tolerance (Phills *et al.,* 1979; Maas, 1986). More importantly, diversity in salt tolerance at intra-specific level has also been found in a considerable number of crop species, for example, barley (Epstein & Norlyn, 1977), soybean (Abel & McKenzie, 1964), rice (Akbar *et al.,* 1972), lucerne (Al-Khatib *et al.,* 1994), triticale (Norlyn & Epstein, 1984), oats (Verma & Yadava, 1986), millets (Kebebew & McNeilly, 1995), and sorghum (Azhar & McNeilly, 1987).

Further work carried out in order to investigate the genetic basis of aluminium tolerance in rice (Howeler & Cadavid, 1976), wheat (Camargo, 1981; Aniol, 1990), sorghum (Boye-Goni & Marcarian, 1985; Gourley *et al.,* 1990) and soybean (Bianchi-Hall *et al.,* 1998), revealed that aluminium tolerance was controlled by the genes acting additively and non additively. However, evidence about the genetic basis of manganese tolerance is very meagre. The studies reported on the genetic basis of variation for salinity tolerance in different crop species are relatively few in numbers. The available evidences, for example, in sorghum (Azhar & McNeilly, 1988, 1989), rice (Gregoria & Senadhira, 1993), pearl millet (Kebebew & McNeilly, 1996), and tomato (Foolad, 1996), revealed that tolerance in these species was predominantly under genetic control. In *Medicago sativa* salt tolerance is highly heritable (Noble *et al.,* 1984) and a significant improvement was made after two generations of selection, whilst Allen *et al.* (1985) working with the same species found h^2_{BS} of the character at the germination stage to be 50%.

Tolerance to increased concentration of copper and zinc in *Agrostis tenuis* proved to be heritable (Gartside & McNeilly, 1974b), and additive genetic variation for tolerance to high levels of copper was observed within tolerant ecotypes of *Agrostis stolonifera* (Wu *et al.,* 1975). Evidences on the occurrence of variation for aluminium and manganese tolerance are extensively available, and plants differ both between and within the species responses. Foy (1988) categorised 23 species according to their tolerance to aluminium and manganese toxicity. However, tolerance to aluminium in barley was shown to be controlled by a single dominant gene (Reid, 1970), and in wheat by one or more major and modifying genes (Kerridge & Kronstad, 1968).

Physiological mechanisms of stress tolerance. Plant responses to salinity are in general extremely complex, and an array of physiological mechanisms is involved in enabling them to cope with these adverse environmental conditions (Wyn Jones, 1981). It has been argued, particularly by plant physiologists, that development of crop cultivars adapted to saline soils either by selection from existing cultivars or through exploiting general variability through breeding, requires an understanding of the physiological basis of salinity tolerance in plants.

High concentrations in the growing medium may depress growth of most crop plants either by a) lowering water potential (osmotic effects), b) excessive accumulation of ions (toxic effects), or c) effects of specific ions on metabolic processes ranging from absorption of nutrients to enzyme activation or inhibition (Kingsbury *et at*, 1984).

Plants tolerant of salinity adjust to osmotic stress by both uptake and accumulation of ions and synthesis of organic solutes. Increased salt concentration in the rooting medium of plants causes water potential to decrease to the extent that water supply to the plant is severely impaired. The resulting differential potential developed between plants and the salinized medium causes water to flow from the plants into the root zone, and ultimately loss of water results in dehydration, adversely affecting physiological plant activities (Steponkus, 1980).

To facilitate breeding for salt tolerance, adoption of new selection criteria based on knowledge of the physiological mechanisms or characters contributing to salt tolerance has been proposed (Yeo & Flowers, 1990). Partial exclusion of ions and synthesis of organic solutes are the broad physiological mechanisms by which cultivated crops respond to salt stress. However, physiological and biochemical mechanisms of stress tolerance in general, and aluminium and manganese tolerance in particular, are still not well defined, despite these being actively investigated in many parts of the world (Taylor, 1991; Foy, 1997). Increased understanding of these processes would help develop crop cultivars with improved tolerance. For generating salinity resistance in rice, Flowers and Yeo (1995) has proposed pyramiding of resistant genes using physiological markers. Reviewing the physiology of stress tolerance, Larcher (1995) has proposed some non-specific physiological mechanisms that follow a stereotypic pattern, whatever the nature of stress factor is. Accumulation of organic solutes such as free amino acids, proline, and carbohydrates, under stress conditions are among those non-specific mechanisms (Khan *et al*., 2000). Proline and glycine-betain have been found to reduce the toxic effects of NaCl for helical destabilisation at DNA replication (Rajendrakumar *et al*., 1997).

Molecular markers as a selection criteria. A good deal of progress has been made in crop agriculture using conventional methods of breeding crop varieties despite non-availability of knowledge about the physiological and biochemical mechanisms. However, in some situations, genetic advance through breeding plants has been slow due to complex and ambiguous natures of the trait(s), such as stress tolerance. A more comprehensive understanding of physiological and biological mechanisms would contribute positively and efficiently to breed crops suitable for stress conditions. Molecular analysis of the genome at the DNA level can provide a greater advantage because DNA sequences are the same in all of the living cells of a plant, regardless of physiological or developmental state of the tissue. DNA marker technology has provided a new source of information and an impetus for modifying some plant breeding methods. DNA marker technology is a new source of information, and now is being integrated into existing plant breeding programmes all over the world, to facilitate researchers for transferring and combining desirable genes at a rate and precision not previously thought of (Mohan *et al.,* 1997). Restriction Fragment Length Polymorphism (RFLP) mapping, Random Amplified Polymorphic DNA (RAPD) mapping, and Quantitative Trait Loci (QTL) analysis have been developed as advanced techniques to obtain meaningful data about the gene complement governing tolerance phenotypes. Marker-assisted selection (MAS) can be used successfully to pyramid the major genes for salinity tolerance (Bohnert & Jensen, 1996).

With the advent of the polymerase chain reaction (PCR) technique DNA marker system gained a new impetus, and in this way several techniques became available to the research workers to generate genetic markers. These techniques have the potential to make effective selection of complex traits in early generations. Haiyuan *et al.* (1998) used RAPDs and demonstrated that a single major dominant gene controls salt tolerance in rice. Similarly, Foolad and Chen (1998) identified 13 RAPD markers at eight genomic regions that were associated with quantitative trait loci (QTL) affecting salt tolerance during germination in tomato. They concluded that simultaneous or sequential transfer of QTL at different developmental stages would improve salt tolerance throughout the ontogeny of a crop cultivar.

CONCLUSIONS

In view of the increasing pressure of population throughout the world, particularly in developing countries, plant breeders and geneticist are obliged to look for ways and means to harvest handful grains from the derelict lands. To persue the breeding efforts effectively an understanding of the physiological and molecular bases of stress tolerance may provoke more active research through the collaborative efforts of plant breeders, physiologists and molecular biologists. Future work should include more emphasis on the engineering of metabolic pathways into crop plants, and the development of transgenic plants useful in conventional breeding programmes. The use of transgenic plants would not only be a step forward towards improving stress tolerance in crop plants, but their use in physiological studies would also add to the knowledge about the mechanisms controlling responses to stresses due to different causes.

REFERENCES

Abel, G.H. and A.J. McKenzie, 1964. Salt tolerance of soybean varieties (*Glycine max* L. Merrill) during germination and later growth. *Crop Sci.,* 4: 157–61.

Akbar, M., T. Yabuno and S. Nakao, 1972. Breeding for saline resistant varieties of rice. I. Variability for salt tolerance among some rice varieties. *Japan J. Breed.,* 22: 277–84.

Allen, S.G., A.K. Dobrenz, M.H. Schonhorst and J.E. Stoner, 1985. Heritability of NaCl tolerance in germinating alfalfa seeds. *Agron. J.,* 77: 99–101.

Al-Khatib, M., T. McNeilly and J.C. Collins, 1994. Between and within cultivar variability in salt tolerance in lucerne, (*Medicago sativa* L.). *Genetic Resources and Crop Evolution,* 41: 159–64.

Aniol, A., 1990. Genetics of tolerance to aluminium in wheat (*Triticum aestivum* L Thell). *Plant and Soil,* 123: 223–27.

Azhar, F.M. and T. McNeilly, 1987. Variability for salt tolerance in *Sorghum bicolor* (L.) Moench under hydroponic conditions. *J. Agron. Crop Sci.,* 159: 269–77.

Azhar, F.M. and T. McNeilly, 1988. The genetic basis of variation for salt tolerance in *Sorghum bicolor* (L.) Moench seedlings. *Pl. Breed.,* 101: 114–21.

Azhar, F.M. and T. McNeilly, 1989. The response of four sorghum accessions/ cultivars to salinity during whole plant development. *J. Agron. Crop Sci.,* 163: 33–43.

Bianchi-Hall, C. M., E. Thomas, Jr. Carter, T.W. Rufty, C. Arellano, H.R. Boerma, D.A. Ashley and J.W. Burton, 1998. Heritability and resource allocation of aluminium tolerance from soybean PI 416937. *Crop Sci.,* 38: 513–22.

Bohnert, H.J. and R.G. Jensen, 1996. Metabolic engineering for increased salt tolerance - The next step. *Australian J. Pl. Physiol.,* 23: 661–67.

Boye-Goni, S.R. and V. Marcarian, 1985. Diallel analysis of aluminium tolerance in selected lines of grain sorghum. *Crop. Sci.,* 25: 749–52.

Bradshaw, A.D. and K. Hardwick, 1989. Evolution and stress – genotypic and phenotypic components. *Biol. J. Linn. Soc.,* 37: 137–55.

Bradshaw, A.D. and T. McNeilly, 1981. *Evolution and Pollution*. Edward Arnold, London.

Breburda, J., 1990. Development of agricultural yield levels and soil K-status in Eastern and Western Europe. In: *Development of K Fertiliser Recommendations*. pp. 17–35. International Potash Institute, Switzerland.

Camargo, C.E.O., 1981. Wheat breeding. I. Inheritance of tolerance to aluminium toxicity in wheat. *Bragantia,* 40: 33–45.

Clark, R.B. and R.R. Duncan, 1993. Selection of plants to tolerate soil salinity, acidity, and mineral deficiencies. *Int. Crop Sci.,* 1: 371–79.

Epstein, E. and J.D. Norlyn, 1977. Seawater based crop production: A feasibility study. *Science,* 197: 249–51.

Epstein, E., J.D. Norlyn, D.W. Rush, R.W. Kingsbury, D.W. Kelley, G.A. Cunningham and A.F. Wrona, 1980. Saline culture of crops: A genetic approach. *Science,* 210: 399–404.

FAO, 1998. World Agriculture Information Centre. FAOSTAT (Web site). *www.fao.org/waicent/faostat.htm*.

Flowers, T.J. and A.R. Yeo, 1995. Breeding for salinity resistance in crop plants: where next? *Australian J. Pl. Physiol.,* 22: 875–84.

Foolad, M.R., 1996. Genetic analysis of salt tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. *Pl. Breed.,* 115: 245–50.

Foolad, M.R. and F.Q. Chen, 1998. RAPD markers associated with salt tolerance in an interspecific cross of tomato (*Lycopersicon esculentum* x *L. pennellii*). *Plant Cell Reports,* 17: 306–12.

Foy, C.D., 1974. Effect of aluminium on plant growth. In: Carson, E. W. (Ed.). *The Plant Growth and Its Environment*. pp. 601–42. University Press of Virginia, Charlottesville. USA.

Foy, C.D., 1988. Plant adaptation to acid, aluminium toxic soils. *Commun. Soil and Plant Analysis,* 19: 959–87.

Foy, C.D., 1997. Tailoring plants to fit problem soils-progress and problems for future research. In: Moniz, A.C. *et al*. (Eds.). *Plant-soil Interactions at low pH: Sustainable Agriculture and Forestry Production*. Brazilian Soil Science Society pp. 55–7.

Foy, C.D., B.J. Scott and J.A. Fisher, 1988. Genetics and breeding of plants tolerant to manganese toxicity. In: Graham, R.D. *et al*. (Eds.) *Manganese in Soil and Plants* pp. 261–76. Kluwer Acad. Publishers, Boston, USA.

Gartside, D.W. and T. McNeilly, 1974a. Genetic studies in heavy metal tolerant plants. I. Genetics of zinc tolerance in *Anthoxanthum odoratum. Heredity* 32: 287–99.

Gartside, D.W. and T. McNeilly, 1974b. Genetic studies in heavy metal tolerant plants. II. Zinc tolerance in *Agrostis tenuis. Heredity* 33: 303–308.

Gourley, L.M., S.A. Rogers, C. Ruiz-Gomes and R.B. Clark, 1990. Genetic aspects of aluminium tolerance in sorghum. *Plant and Soil*, 123: 211–6.

Gregoria, G.B. and D. Senadhira, 1993. Genetic analysis of salinity tolerance in rice (*Oryza sativa* L.). *Theor. Appl. Genet.,* 86: 333–8.

Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley, Chichester.

Haiyuan, D., Z. Gengyun, G. Yan, C. Shaolin and C. Shouyi, 1998. RAPD tagging of salt tolrant genes in rice. *Chinese Sci., Bull.,* 43: 330–32.

Haug, A., 1984. Molecular aspects of aluminium toxicity. *Critical Rev. Pl. Sci.,* 1: 345–73.

Howeler, R.H. and L.F. Cadavid, 1976. Screening of rice cultivars for tolerance to Al toxicity in nutrient solutions as compared with a field screening method. *Agron. J.,* 68: 551–5.

Jackson, T.L. and H.M. Reisenauer, 1984. Crop response to lime in western United States. In: Adams, F. (Ed.). *Soil Acidity and Liming*. pp. 333–47. ASA, CSSA, SSSA, Madison, WI, USA.

Jones, H.G. and M.B. Jones, 1989. Some terminology and common mechanisms. In: Jones, H. G. *et al*. (Eds.). *Plants Under Stress*. Cambridge University Press: Cambridge.

Kebebew, F. and T. McNeilly, 1995. Variation in response of accessions of minor millets, *Pennisetum americanum* (L.) Leeke (Pearl Millet) and *Eleusine coracana* (L.) Gaertn (Finger Millet), and *Eragrostis tef* (Zucc.) Trotter (Tef), to salinity in early seedling growth. *Plant and Soil,* 175: 311–21.

Kebebew, F. and T. McNeilly, 1996. The genetic basis of variation in salt tolerance in Pearl millet, *Pennisetum americanum* (L.) Leeke. *J. Genet. Breed.,* 50: 129–36.

Kerridge, P.C. and W.E. Kronstad, 1968. Evidence of genetic resistance to aluminium toxicity in wheat. (*Triticum aestivum* Vill., Host). *Agron. J.,* 60: 710–11.

Khan, A.A., T. McNeilly and J.C. Collins, 2000. Accumulation of amino acids, proline, and carbohydrates in response to aluminium and manganese stress in maize. *J. Pl. Nutr.,* 23: 1303–14.

Kingsbury, R.W., E. Epstein and R.W. Pearcy, 1984. Physiological responses to salinity in selected lines of wheat. *Pl. Physiol.,* 74: 417–23.

Larcher, W., 1995. *Physiological Plant Ecology*. 3rd Ed. Springer, London.

Maas, E.V., 1986. Salt tolerance of plants. *Appl. Agric. Res.,* 1: 12–26.

McNeilly, T., 1994. Metal toxicity. In: Yeo, A.R. and T.J. Flowers (Eds.). *Monographs on Theoretical and Applied Genetics*, 21, pp. 145–74. Springer-Verlag, Berlin Heidelberg.

Mohan, M., S. Nair, A. Bhagwat, T.G. Krishna, M. Yano, C.R. Bhatia, and T. Sasaki, 1997. Genome mapping, molecular markers and marker-assisted selection in crop plants. *Molecular. Breed.,* 3: 87–103.

Noble, C.L., G.M. Halloram and D.W. West, 1984. Identification and selection for salt tolerance in lucerne (*Medicago sativa* L.). *Australian J. Agric. Res.,* 35: 239–52.

Norlyn, J.D. and E. Epstein, 1984. Variability in salt tolerance of four *triticale* lines at germination and emergence. *Crop Sci.,* 24: 1090–92.

Parker, D.R., T.B. Kinraide and L.W. Zelazny, 1989. On the phytotoxicity of polynuclear hydroxy-aluminium complexes in soil. *Science Soc. Amer. J.,* 53: 789–96.

Phills, B.R., N.H. Peck, G.E. MacDonald and R.W. Robinson, 1979. Differential response of *Lycopersicon* and *Solanum* species to salinity. *J. Amer. Soc. Hort. Sci.,* 104: 349–52.

Rajendrakumar, C.S.V., T. Suryanarayana and A.R. Reddy, 1997. DNA helix destabilization by proline and betaine: possible role in the salinity tolerance process. *FEBS Letters,* 410: 201–5.

Reid, A.D., 1970. Genetic control of reaction to aluminium in winter barley. In: Nilan, R. A. (Ed.) *Barley Genetics II*. Proc. 2nd Int. Barley Genetic Symposium pp. 409–13. Washington State University Press, Pullman.

Shalhevet, J.E. and B. Yaron, 1973. Effect of soil and water salinity on tomato growth. *Plant and Soil,* 39: 285–92.

Shalhevet, J.E., E.V. Maas, G.H. Hoffmanand and G. Ogata, 1976. Salinity and the hydraulic conductance of roots. *Physiological Plant* 38: 224–32.

Shannon, M.C., 1984. Breeding, selection, and the genetics of salt tolerance. In: Staples, R. C., and G. A. Toeniessen (Eds.). *Salinity Tolerance in Plants-Strategies for Crop Improvement*, pp. 231-54. Wiley, New York, USA.

Singh, N.T., 1992. Dry land salinity in the Indo-Pakistan sub-continent. In: Derange, H.E. (Ed.). *Degradation and Restoration of Arid Lands*. pp. 179–248. Texas Technical University, Lubbock, USA.

Steponkus, P.L., 1980. A unified concept of stress in plants. In: Rains, D. W. *et al*. (Eds.), *Genetic engineering of osmoregulation: Impact on Plant Productivity for Food, Chemicals and Energy*. pp. 235. Plenum Press, N. York.

Szabolcs, I., 1987. The global problems of salt-affected soils. *Acta Agon. Hung.,* 36: 159–72.

Szabolcs, I., 1993. Soils and salinisation. In: Pessarakli, M. (Ed), *Handbook of Plant and Crop Stress*. pp. 3–11. Marcel, Dekker, Inc, New York.

Tanji, K.K., 1990. Nature and extent of agricultural salinity. In: Tanji, K.K. (Ed.) *Agriculture Assessment and Management*. pp, 1–17. American Society of Civil Engineering, New York.

Taylor, G.J., 1991. Current views of the aluminium stress response; the physiological basis of tolerance. *Current Topics in Plant Biochemistry and Physiology,* 10: 57–93.

Verma O.P.S. and R.B.R. Yadava, 1986. Salt tolerance of some oats (*Avena sativa*) varieties at germination and seedling stage. *J. Agron. Crop Sci.,* 156: 123–7.

von Uexkull, H.R. and E. Mutert, 1995. Global extent, development and economic impact of acid soils. *Plant and Soil,* 171: 1–15.

Williams, J.G.K., A.R. Kubelic, K.J. Livak, J.A. Rafalsky and S.V. Tingey, 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucleic Acid Res.,* 18: 6531–5.

Woolhouse, H., 1983. Toxicity and tolerance in the response of plants to metals. In: Lange, O.L. *et al*. (Eds.). *Physiological Plant Ecology. III. Response to the chemical and biological environment*. pp. 254. Springer Berlin, Heidelberg.

Wright, R.J., V.C. Baligar, K.D. Ritcheyand and S.F. Wright, 1989. Influence of soil solution aluminium on root elongation of wheat seedlings. *Plant and Soil,* 113: 294–8.

Wu, L., A.D. Bradshaw and A.D. Thurman, 1975. The potential for evolution of heavy metal tolerance in plants. III. The rapid evolution of copper tolerance in *Agrostis stolonifers*. *Heredity* 34: 165–87.

Wyn Jones, R.G., 1981. Salt tolerance. In: Johnson, C.B. (Ed.). *Physiological Processes Limiting Plant Productivity*. pp, 271–91. Butterworth, London.

Yeo, A.R. and T.J. Flowers, 1990. Screening of rice (*Oryza sativa* L.) genotypes for physiological characters contributing to salinity resistance, and their relationship to overall performance. *Theor. Appl. Genet.,* 79: 377–84.

Zeigler, R.S., S. Pandey, J. Miles, L.M. Gourley and S. Sarkarung, 1995. Advances in the selection and breeding of acid-tolerant plants: Rice, maize, sorghum and tropical forages. In: Date R. A. (Ed.). *Plant Soil Interactions at low pH*. pp. 391–406. Kluwer Acad. Publishers. The Netherlands.

(Received 22 March 2001; Accepted 28 March 2001)