



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Agricultural Water Management 78 (2005) 15–24

---

---

Agricultural  
water management

---

---

[www.elsevier.com/locate/agwat](http://www.elsevier.com/locate/agwat)

# Why does salinity pose such a difficult problem for plant breeders?

T.J. Flowers\*, S.A. Flowers

*School of Life Science, John Maynard Smith Building, University of Sussex, Falmer, Brighton, East Sussex BN1 9QG, UK*

Accepted 1 April 2005

Available online 13 June 2005

---

## Abstract

The dominance of salt water across the surface of the earth has led to the widespread occurrence of salt-affected soils. Salt-tolerant plants (halophytes) have evolved to grow on these soils, with halophytes and less tolerant plants showing a wide range of adaptations. However, most of our crops are salt-sensitive. Consequently, salinity is an ever-present threat to agriculture, especially in areas where secondary salinisation has developed through irrigation or deforestation. Attempts to improve the salt tolerance of crops have met with very limited success, due to the complexity of the trait, both genetically and physiologically. Tolerance shows all the characteristics of a multigenic trait, with quantitative trait loci (QTLs) identified in barley, citrus, rice and tomato.

Attempts to produce salt-tolerant crops have involved both the domestication of halophytes and the manipulation of existing crop species through conventional breeding programmes, the use of in vitro selection, pooling physiological traits, interspecific hybridisation, the use of marker-aided selection and the development of transgenic plants. After 10 years of research, the value of using transgenic plants to alter salt tolerance has yet to be tested in the field. The use of physiological traits in breeding programmes and the domestication of halophytes currently offer viable alternatives to the development of tolerance through the use of transgenic technologies.

© 2005 Elsevier B.V. All rights reserved.

*Keywords:* Salinity; Plant breeding

---

\* Corresponding author.

*E-mail address:* [t.j.flowers@sussex.ac.uk](mailto:t.j.flowers@sussex.ac.uk) (T.J. Flowers).

## 1. Introduction

Almost three quarters of the surface of the earth is covered by salt water and so it is not surprising that salts affect a significant proportion of the world's land surface. These salt-affected areas fall broadly into two categories: sodic and saline. Sodic soils are dominated by excess sodium on exchange sites and a high concentration of carbonate/bicarbonate anions; they have a high pH (greater than 8.5 and perhaps up to 10.8) with a high sodium absorption ratio (SAR) and poor soil structure. Saline soils are again generally dominated by sodium ions, but with the dominant anions being chloride and sulphate; pH values and SARs are much lower and electrical conductivities higher ( $>4 \text{ dS m}^{-1}$ ) than in sodic soils. Salt-affected soils contain sufficient concentrations of soluble salts to reduce the growth of most plant species.

Naturally occurring salt-affected soils cover about a billion hectares; these areas, which are largely coastal salt marshes or inland deserts, are not as important to agriculture as the areas of secondary salinisation brought about through irrigation and forest clearance. There is currently nearly 275 million hectares of irrigated land (273 Mha in 2001; <http://apps.fao.org>, January 2004) of which about 20% is salt affected (see for example Ghassemi et al., 1995); perhaps half of all irrigation schemes are subject to salinisation. This is particularly unfortunate, as it is irrigated land that is the most productive in world agriculture. An increasing problem, particularly in Australia, is dryland salinity (Beresford et al., 2001; Munns et al., 2002), which affects about 2 million hectares of Western Australia with a further 6 million hectares at risk. Dryland salinity is linked to rising water tables brought about by increased deep drainage of rainfall following forest clearance and a change from deep-rooted perennial plants to a shallow-rooted annual crop (wheat).

Salt-affected land is not, however, entirely inimical to plant growth. Salt tolerance has evolved and there are naturally occurring salt-tolerant trees (mangroves), shrubs, grasses and herbs. However, virtually none of our crop plants is able to tolerate even a quarter of seawater without loss of yield. Consequently, salinisation is a problem for agriculture. But, if there are naturally salt-tolerant plants, why should salt-affected soils cause an agricultural problem? The reason lies in the complexity of salt tolerance.

## 2. What makes a halophyte salt tolerant?

For convenience, plants have been divided into two groups: the salt-sensitive glycophytes and the salt-tolerant halophytes, although in reality one group merges into the other. Nonetheless, the division is useful in that the true halophytes can be used as models in which the range of their adaptations and their importance can be evaluated. Although salt-tolerant plants occupying terrestrial habitats come from a wide spectrum of families (Flowers et al., 1977), two families are particularly important, the Chenopodiaceae and the Poaceae. Members of these families provide models through which the physiology of salt tolerance can be understood.

The primary environmental factor faced by plants growing in salt marshes and salt deserts is the high concentration of salts that they encounter; soil water potentials can be lowered by the equivalent of about  $-1$  to  $-2.5 \text{ MPa}$  ( $-5 \text{ MPa}$  in extreme conditions) by the salts present

in the soil. For these saline environments (that is excluding the extreme salt deserts), the plant water potential must then be lowered by an equivalent of up to about 500 mM NaCl (Flowers, 1985). This is achieved through adjustment of plant water and solute content. For example where plants may be inundated by seawater they adjust to these low water potentials by accumulating high (more than 500 mM) concentrations of sodium and chloride in their cells. However, the very salts necessary for osmotic adjustment are potentially toxic and so must be separated from the metabolic machinery of the cells. This is achieved by compartmentation: salt-sensitive metabolic processes take place in the cytoplasm, while the salt necessary for osmotic adjustment is stored in vacuoles (Flowers et al., 1986).

Within the cytoplasm, osmotic adjustment is effected by compatible solutes. These are organic compounds, such as glycinebetaine, mannitol and proline, which do not damage (and probably protect) the metabolism (Pollard and Wyn, 1979; Rathinasabapathi, 2000). The process of compartmentation requires that halophytes have a mechanism to maintain differences in ion concentration across the membrane that surrounds their vacuoles; this mechanism depends on membrane structure (Leach et al., 1990) and on the proteins that transport ions across membranes.

Ions enter plant cells through proteins that form an integral part of cell membranes. These proteins can either form channels through which ions diffuse down electrochemical potential gradients or carriers, where the protein binds an ion on one side of the membrane and releases it on the other side. Both processes are driven by energy-consuming ion pumps. These proteins (ion pumps) use the energy stored in ATP (or in the case of the vacuolar membrane, ATP and pyrophosphate) to move protons across the membrane generating a difference of hydrogen ion concentration (pH) and electrical potential ( $\Delta E$ ). It is the difference in electrical potential that drives the inward movement of cations through channels and the difference in hydrogen ion concentration that drives the movement of ions through carriers—to which protons and ions bind.

In spite of considerable knowledge of the way in which potassium ions cross membranes, it is not clear how sodium (or chloride) enters plant cells. Although it is generally thought that sodium is 'mistaken' for potassium by potassium carriers or channels, it is also possible that sodium enters cells through non-selective cation channels, particularly those activated by glutamate (Demidchik et al., 2002; Maathuis and Amtmann, 1999; Maser et al., 2002). It is also apparent that in some plants, ions can reach the leaves through pathways that bypass the controls that normally force ions through a specialised layer of cells in the roots known as the endodermis. If there are breaks in the endodermis, water and dissolved solutes can flow to the leaves without encountering the selective barriers of cell membranes. This so-called 'bypass flow' is potentially dangerous and normally contributes little to the net transport of ions to the shoots (Perry and Greenway, 1973). However, if external concentrations are high – for example of sodium and chloride in the case of salinity – even a small fraction of the transpiration stream bypassing endodermal (cytoplasmic) control can lead to significant quantities of ions reaching the shoots. This pathway appears to be particularly important in paddy rice (Garcia et al., 1997; Yeo et al., 1987).

Halophytes must balance their requirement for the salts needed for osmotic adjustment with their growth rate (Flowers and Yeo, 1986). Regulating transpiration plays an important part in this process, as it is the transpiration stream that carries ions between root and shoot. Consequently, factors that influence the rate of water loss by plants are important

in salt tolerance. Many halophytes show morphological adaptations associated with limiting transpiration, such as reduced leaves (which may be ‘fleshy’ or ‘succulent’). In some species, an additional feature has evolved to regulate leaf ion concentrations. The leaf epidermis carries modified cells (salt glands) that secrete excess salt from the leaves (Thomson et al., 1988).

### 3. How does salinity affect glycophytes?

Halophytes, although widespread taxonomically, are relatively rare amongst the 250,000 species of flowering plants and virtually all of our crops are glycophytes. There is, however, considerable variability in the tolerance of these glycophytes to salt. Variation occurs between species and has been quantified for crops (Francois and Maas, 1994; Maas and Hoffmann, 1976) and within species (e.g. Bernstein and Ayers, 1953; Datta, 1972; Flowers and Yeo, 1981; Greenway, 1962). Glycophytes, if they are to survive salinity, must adapt to the external salt concentrations; they face the same problems as those faced by halophytes.

Salinity has three potential effects on plants:

- lowering of the water potential,
- direct toxicity of any Na and Cl absorbed and
- interference with the uptake of essential nutrients.

The latter might not be expected to have an immediate effect on plant growth as plants have reserves of nutrients that they can mobilise. However, when salt is first encountered by a plant, there are two phases to its response. The first phase is a response to the changed water relations brought about by the lowering of the external water potential by the salt. These initial effects of salinity (phase 1, due to a change in water potential) are likely to be the same for cultivars of differing salt tolerance. Only as ions are accumulated over time (phase 2) do true differences in salt tolerance appear (Munns, 1993). Sensitive cultivars accumulate ions more quickly than tolerant cultivars and this ion accumulation leads to leaf death and, progressively, death of the plant (Munns, 2002).

The adaptations required to survive in salt-affected soils are the same in all plants. Such adaptations are at their most extreme in halophytes, but can be found to differing degrees, in glycophytes. Salt tolerance depends upon:

- morphology;
- compartmentation and compatible solutes;
- regulation of transpiration;
- control of ion movement;
- membrane characteristics;
- tolerating high Na/K ratios in the cytoplasm;
- salt glands.

With so many factors involved, it is to be expected that salt tolerance would depend on the action of many genes.

#### 4. Genetics of salt tolerance

What then is the evidence that salt tolerance is determined by a number of genes? Many genes have a visible phenotype; the effects of changes in the activity of these genes are obvious to a visual assessment. The classical examples of plant genetics are those outlined more than 100 years ago by Mendel, such as the cross between round yellow peas and wrinkled green peas: the resulting offspring are either round-yellow peas, round-green, wrinkled-yellow or wrinkled-green (and in a ratio of 9:3:3:1). Characters, such as round or wrinkled, are determined by a single pair of alleles: one is dominant over the other. Similar allelic pairs control many characters; other examples are two or six rows of seed in barley or the presence of rough or smooth awns. These characters are said to be qualitative characters and to display qualitative inheritance. However, this is by no means always the case. Other characters, such as cob length in maize, depend on several to many genes; they are said to be quantitative characters. These are called multiple genes, multigenes or polygenes and the characters they determine multigenic or polygenic. There are a number of characteristics of multiple gene inheritance, listed by [Poehlman \(1987\)](#):

- A number of genes at different loci contribute to the quantitative character.
- Each of the multiple genes can have a small effect on the phenotype.
- As the effects of the various genes can be additive or epistatic, the character shows continuous variation.
- The phenotype can be a result of the genotype and its interaction with the environment.
- Following crossing, transgressive segregation (where offspring are outside the range of the parental phenotypes) can arise.

The sodium concentration within the leaves of rice exposed to salinity shows a wide distribution between individuals and transgressive segregation, features of a multigenic character ([Fig. 1](#)).

With the advent of the ability to extract DNA from plants, to break it into fragments with enzymes that cut at specific base sequences and to determine the sequence of those bases, it has proved possible to characterise the DNA of individual plants—to identify their genotype. Combining this DNA technology and advanced statistical methods ([Kearsey, 1998](#)), chromosomal regions that contain the genes that determine quantitative traits can be identified: these are called quantitative trait loci or QTLs. So, by crossing parents that differ in one or more aspects of salt tolerance (their phenotype), and then analysing the phenotype and the genotype of their offspring, it has been possible to locate QTL for salt tolerance ([Table 1](#)). For a plant breeder, such QTLs are particularly attractive, as they can, in principle, be developed to produce markers to aid selection (the process is known as marker-aided selection or marker-assisted selection, MAS). Such markers can be used in the selection of lines following a crossing programme and without the need to determine their phenotype (that is without the need to evaluate performance of plants under stress) or to take all the lines to seed ([Asins, 2002](#)). The earliest analysis for salt tolerance involved a cross between the cultivated tomato, *Lycopersicon esculentum* and a wild relative, *Lycopersicon pimpinellifolium* (grown under a salinity of 15 dS/m), where QTL for average fruit weight, fruit number and total

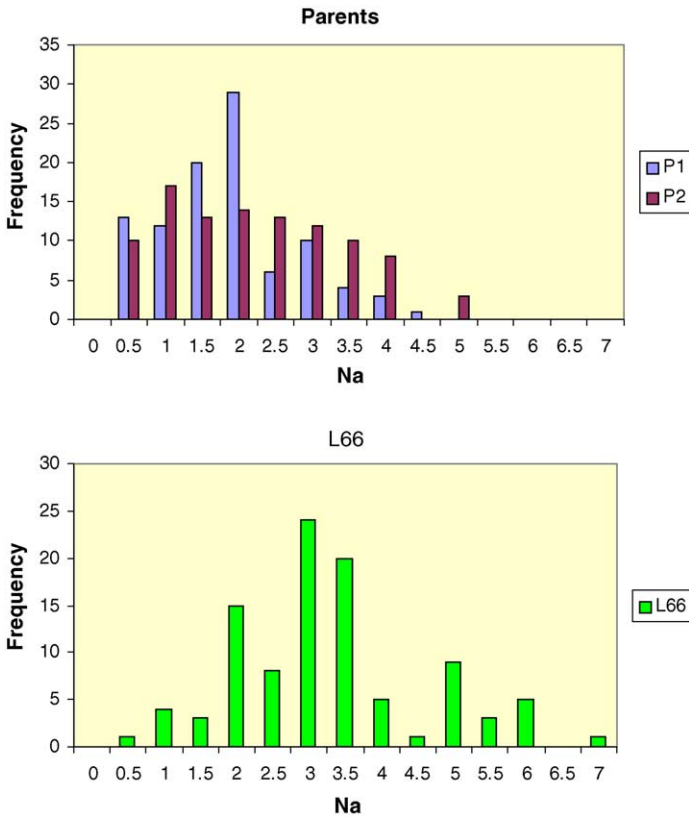


Fig. 1. The sodium concentrations in the parents (P1, IR4630-22-2-5-1-3 and P2 IR15324-117-3-2-2) of a cross (IR55178) of rice (*Oryza sativa*) and one line of offspring (L66). Seedlings were grown hydroponically and after 10 days, sodium chloride added to produce a concentration of 50 mM. After a further 12 days, the concentration was raised to 100 mM for a further 8 days and then the plants harvested. The amount of sodium (Na; mmol per g dry weight) was calculated for each plant. Further details of the experiment can be found in Koyama et al. (2001).

weight were identified (Breto et al., 1994; Table 1). Further analysis showed that such QTL were, however, dependent on the conditions under which the plants were grown (Foolad et al., 1999; Monforte et al., 1997b; Table 1), indicating that different aspects of the physiology determined yield characteristics under different environmental conditions. This finding has been repeated for rice and citrus and suggests that if any particular QTL were to be chosen as marker for the purposes of plant breeding, then care would have to be taken over its choice and the growth conditions. The analyses that have been performed also suggest that QTL associated with salt tolerance vary with the developmental stage at which the analysis is performed in species as widely divergent as tomato, rice and barley, citrus and arabidopsis (Table 1). A further limitation to the use of QTL in plant breeding is the fact that QTL may be specific to particular crosses, a finding reported for both tomato (Monforte et al., 1997a) and rice (Flowers et al., 2000). For rice,

Table 1

Species and traits associated with the effects of salinity for which quantitative trait loci (QTL) have been identified

Species	Trait	Comment	Reference
Tomato	Fruit yield under salinity		Breto et al. (1994)
Tomato	Fruit yield under salinity	QTL dependent on parentage	Monforte et al. (1997a)
Tomato	Fruit yield under salinity	QTL dependent on salinity	Monforte et al. (1997b)
Tomato	Seed germination	QTL dependent on salinity	Foolad et al. (1999)
Citrus	Growth	QTL dependent on salinity	Tozlu et al. (1999a)
Rice	Seedling survival	QTL dependent on salinity	Gong et al. (1999)
Rice	Agronomic traits	QTL dependent on salinity	Gong et al. (2001)
Citrus	Growth (dry matter)	QTL dependent on salinity	Tozlu et al. (1999a)
Tomato	Germination and vegetative growth	Varies with stage of development	Foolad (1999); Foolad and Chen (1999); Foolad et al. (1998); Foolad et al. (1997)
Arabidopsis	Germination and vegetative growth	Varies with stage of development	Quesada et al. (2002)
Barley	Germination and vegetative growth	Varies with stage of development	Mano and Takeda (1997)
Rice	Germination and vegetative growth	Varies with stage of development	Prasad et al. (2000)
Citrus	Ion transport		Tozlu et al. (1999b)
Rice	Ion transport		Koyama et al. (2001)

none of the markers found in one cross showed any association with similar traits in a closely related population of recombinant inbred lines or in selections of a cultivar. It was argued that whilst markers will be of value in using elite lines from the mapping population in backcrossing, the result cautions against any expectation of a general applicability of markers for physiological traits.

## 5. The way forward

Given the complexity of the physiology and the genetics of salt tolerance, is it going to be possible to generate salt-tolerant crops? Certainly, there was only limited success to the mid-1990s (Flowers and Yeo, 1995) and there has been little progress since then. A variety of approaches has been advocated, including conventional breeding, wide crossing, the use of physiological traits and, more recently, marker-assisted selection and the use of transgenic plants. None of these approaches could be said to offer a universal solution. Conventional breeding programmes have rarely delivered enhanced salt tolerance (Flowers and Yeo, 1995), while wide crossing generally reduces yield to unacceptably low levels (Yeo and Flowers, 1989). There has been success using physiological criteria as the basis of selection or rice (Dedolph and Hettel, 1997) and such an approach has recently been advocated for wheat (Munns et al., 2002). A recent analysis has shown that while it is possible to produce a wide range of transgenic plants where some aspect of a trait relating to salt tolerance was altered, none has been tested in the field and few claims for success meet even minimal criteria required to demonstrate enhanced tolerance (Flowers, 2004).

## 6. Summary and conclusions

It is conceivable that approaches that identify specific genes that are up- or down-regulated, either through the analysis of RNA or proteins, might provide a focus for transformation, although we are currently far from choosing key genes for tolerance. Transgenic technology will undoubtedly continue to aid our search for the cellular mechanisms that underlie salt tolerance, but the complexity of the trait is likely to mean that the road to engineering tolerance into sensitive species will be long. This is why generating salt tolerance is proving such a difficult task for plant breeders. In the meantime, it would be expedient to continue to invest in other avenues such as the manipulation of ion excretion from leaves through salt glands, the use of physiological traits in breeding programmes and the domestication of halophytes.

## References

- Asins, M.J., 2002. Present and future of quantitative trait locus analysis in plant breeding. *Plant Breed.* 121, 281–291.
- Beresford, Q., Bekle, H., Phillips, H., Mulcock, J., 2001. *The Salinity Crisis Landscapes, Communities and Politics*. University of Western Australia, Crawley, Western Australia, 324 pp.
- Bernstein, L., Ayers, A.D., 1953. Salt tolerance in five varieties of carrots. *Proc. Am. Soc. Hort. Sci.* 61, 361–366.
- Breto, M.P., Asins, M.J., Carbonell, E.A., 1994. Salt tolerance in *Lycopersicon* species 3. Detection of quantitative trait loci by means of molecular markers. *Theor. Appl. Genet.* 88, 395–401.
- Datta, S.K., 1972. A study of salt tolerance of twelve varieties of rice. *Curr. Sci.* 41, 456–457.
- Dedolph, C., Hettel, G. (Eds.), 1997. *Rice varieties boost yield and improve saline soils. Partners Making a Difference*. IRRRI, Manila, p. 37.
- Demidchik, V., Davenport, R.J., Tester, M., 2002. Nonselective cation channels in plants. *Annu. Rev. Plant Biol.* 53, 67–107.
- Flowers, T., Troke, P., Yeo, A., 1977. The mechanisms of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.* 28, 89–121.
- Flowers, T.J., 2004. Improving crop salt tolerance. *J. Exp. Bot.* 55, 1–13.
- Flowers, T.J., 1985. Physiology of halophytes. *Plant Soil* 89, 41–56.
- Flowers, T.J., Hajibagheri, M.A., Clipson, N.J.W., 1986. Halophytes. *Q. Rev. Biol.* 61, 313–337.
- Flowers, T.J., Koyama, M.L., Flowers, S.A., Sudhakar, C., Singh, K.P., Yeo, A.R., 2000. QTL: their place in engineering tolerance of rice to salinity. *J. Exp. Bot.* 51, 99–106.
- Flowers, T.J., Yeo, A.R., 1995. Breeding for salinity resistance in crop plants – Where next. *Aust. J. Plant Physiol.* 22, 875–884.
- Flowers, T.J., Yeo, A.R., 1986. Ion relations of plants under drought and salinity. *Aust. J. Plant Physiol.* 13, 75–91.
- Flowers, T.J., Yeo, A.R., 1981. Variability in the resistance of sodium chloride salinity within rice (*Oryza sativa* L.) varieties. *New Phytol.* 81, 363–373.
- Foolad, M.R., 1999. Comparison of salt tolerance during seed germination and vegetative growth in tomato by QTL mapping. *Genome* 42, 727–734.
- Foolad, M.R., Chen, F.Q., 1999. RFLP mapping of QTLs conferring salt tolerance during the vegetative stage in tomato. *Theor. Appl. Genet.* 99, 235–243.
- Foolad, M.R., Chen, F.Q., Lin, G.Y., 1998. RFLP mapping of QTLs conferring salt tolerance during germination in an interspecific cross of tomato. *Theor. Appl. Genet.* 97, 1133–1144.
- Foolad, M.R., Lin, G.Y., Chen, F.Q., 1999. Comparison of QTLs for seed germination under non-stress, cold stress and salt stress in tomato. *Plant Breed.* 118, 167–173.
- Foolad, M.R., Stoltz, T., Dervinis, C., Rodriguez, R.L., Jones, R.A., 1997. Mapping QTLs conferring salt tolerance during germination in tomato by selective genotyping. *Mol. Breed.* 3, 269–277.

- Francois, L.E., Maas, E.V., 1994. Crop response and management on salt-affected soils. In: Pessaraki, M. (Ed.), *Handbook of Plant and Crop Stress*, Marcel Dekker, 270 Madison Ave/New York/NY 10016, pp. 149–181.
- Garcia, A., Rizzo, C.A., UdDin, J., Bartos, S.L., Senadhira, D., Flowers, T.J., Yeo, A.R., 1997. Sodium and potassium transport to the xylem are inherited independently in rice, and the mechanism of sodium: Potassium selectivity differs between rice and wheat. *Plant Cell Environ.* 20, 1167–1174.
- Ghassemi, F., Jakeman, A.J., Nix, H.A., 1995. *Salinisation of Land and Water Resources. Human causes, Extent Management & Case Studies*. University of New South Wales, Sydney, 526 pp.
- Gong, J.M., He, P., Qian, Q.A., Shen, L.S., Zhu, L.H., Chen, S.Y., 1999. Identification of salt-tolerance QTL in rice (*Oryza sativa* L.) *Chin. Sci. Bull.* 44, 68–71.
- Gong, J.M., Zheng, X.W., Du, B.X., Qian, Q., Chen, S.Y., Zhu, L.H., He, P., 2001. Comparative study of QTLs for agronomic traits of rice (*Oryza sativa* L.) between salt stress and nonstress environment. *Sci. China Ser. C-Life Sci.* 44, 73–82.
- Greenway, H., 1962. Plant response to saline substrates. I. Growth and ion uptake of several varieties of *Hordeum* during and after sodium chloride treatment. *Aust. J. Biol. Sci.* 15, 16–39.
- Kearsey, M.J., 1998. The principles of QTL analysis (a minimal mathematics approach). *J. Exp. Bot.* 49, 1619–1623.
- Koyama, M.L., Levesley, A., Koebner, R.M.D., Flowers, T.J., Yeo, A.R., 2001. Quantitative trait loci for component physiological traits determining salt tolerance in rice. *Plant Physiol.* 125, 406–422.
- Leach, R.P., Wheeler, K.P., Flowers, T.J., Yeo, A.R., 1990. Molecular markers for ion compartmentation in cells of higher plants. II. Lipid composition of the tonoplast of the halophyte *Suaeda maritima* (L.) Dum. *J. Exp. Bot.* 41, 1089–1094.
- Maas, E.V., Hoffmann, G.J., 1976. Crop salt tolerance: evaluation of existing data. In: *Proceedings International Conference Texas Technical University*. pp. 187–197.
- Maathuis, F.J.M., Amtmann, A., 1999. K<sup>+</sup> nutrition and Na<sup>+</sup> toxicity: the basis of cellular K<sup>+</sup>/Na<sup>+</sup> ratios. *Ann. Bot.* 84, 123–133.
- Mano, Y., Takeda, K., 1997. Mapping quantitative trait loci for salt tolerance at germination and the seedling stage in barley (*Hordeum vulgare* L.). *Euphytica* 94, 263–272.
- Maser, P., Gierrh, M., Schroeder, J.I., 2002. Molecular mechanisms of potassium and sodium uptake in plants. *Plant Soil* 247, 43–54.
- Monforte, A.J., Asins, M.J., Carbonell, E.A., 1997a. Salt tolerance in *Lycopersicon* species 5. Does genetic variability at quantitative trait loci affect their analysis. *Theor. Appl. Genet.* 95, 284–293.
- Monforte, A.J., Asins, M.J., Carbonell, E.A., 1997b. Salt tolerance in *Lycopersicon* species 6. Genotype-by-salinity interaction in quantitative trait loci detection: constitutive and response QTLs. *Theor. Appl. Genet.* 95, 706–713.
- Munns, R., 2002. Comparative physiology of salt and water stress. *Plant Cell Environ.* 25, 239–250.
- Munns, R., 1993. Physiological processes limiting plant-growth in saline soils – some dogmas and hypotheses. *Plant Cell Environ.* 16, 15–24.
- Munns, R., Husain, S., Rivelli, A.R., James, R.A., Condon, A.G., Lindsay, M.P., Lagudah, E.S., Schachtman, D.P., Hare, R.A., 2002. Avenues for increasing salt tolerance of crops, and the role of physiologically based selection traits. *Plant Soil* 247, 93–105.
- Perry, M.W., Greenway, H., 1973. Permeation of uncharged organic molecules and water through tomato roots. *Ann. Bot.* 37, 225–232.
- Poehlman, J.M., 1987. *Breeding Field Crops*. Van Nostrand Reinhold, New York, 724 pp.
- Pollard, A., Wyn, J.W.G., 1979. Enzyme activities in concentrated solutions of glycinebetaine and other solutes. *Planta* 144, 291–298.
- Prasad, S.R., Bagali, P.G., Hittalmani, S., Shashidhar, H.E., 2000. Molecular mapping of quantitative trait loci associated with seedling tolerance to salt stress in rice (*Oryza sativa* L.) *Curr. Sci.* 78, 162–164.
- Quesada, V., Garcia-Martinez, S., Piqueras, P., Ponce, M.R., Micol, J.L., 2002. Genetic architecture of NaCl tolerance in arabidopsis. *Plant Physiol.* 130, 951–963.
- Rathinasabapathi, B., 2000. Metabolic engineering for stress tolerance: Installing osmoprotectant synthesis pathways. *Ann. Bot.* 86, 709–716.
- Thomson, W.W., Faraday, C.D., Oross, J.W., 1988. Salt glands. In: Baker, D.A., Hall, J.L. (Eds.), *Solute Transport in Plant Cells and Tissues*. Longman Scientific and Technical, Harlow, pp. 498–537.

- Tozlu, I., Guy, C.L., Moore, G.A., 1999a. QTL analysis of morphological traits in an intergeneric BC1 progeny of Citrus and Poncirus under saline and non-saline environments. *Genome* 42, 1020–1029.
- Tozlu, I., Guy, C.L., Moore, G.A., 1999b. QTL analysis of Na and Cl accumulation related traits in an intergeneric BC1 progeny of citrus and Poncirus under saline and non saline environments. *Genome* 42, 692–705.
- Yeo, A.R., Flowers, T.J., 1989. Selection for physiological characters – examples from breeding for salt tolerance. In: Jones, H.G., Flowers, T.J., Jones, M.B. (Eds.), *Plants under Stress Biochemistry, Physiology and Ecology and their Application to Plant Improvement*. Cambridge University Press, Cambridge, pp. 217–234.
- Yeo, A.R., Yeo, M.E., Flowers, T.J., 1987. The contribution of an apoplastic pathway to sodium uptake by rice roots in saline conditions. *J. Exp. Bot.* 38, 1141–1153.