How Can Stomata Contribute to Salt Tolerance?

MICHAEL F. ROBINSON*, ANNE-ALIÊNOR VÉRY†, DALE SANDERS†
and T. A. MANSFIELD*

* Division of Biological Sciences, Institute of Environmental and Biological Sciences, Lancaster University, Lancaster LA1 4YQ and † Department of Biology, University of York, P.O. Box 373, York YO1 5YW, UK

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Although some of the physiological mechanisms which contribute to salt tolerance in plants are known, there are still some major gaps in understanding and it remains impossible to provide a satisfactory integrated picture for the plant as a whole. The operation of stomata in halophytes has received little attention even though all of the salt present in the shoot (apart from that taken in during submergence) is thought to be carried in the transpiration stream. In non-halophytes, stomatal function is damaged by sodium ions, and disruption of the normal regulation of transpiration should be seen as a possible contributor to their inability to survive in salt-laden soils. The development of salt-tolerant cultivars of crops may require attention to the need for appropriate adaptations to the ionic relations of stomatal guard cells. Despite the small amount of evidence available, it is possible to identify two alternative adaptations that occur in the stomata of halophytes: (1) the guard cells can utilize Na⁺ instead of K⁺ to achieve their normal regulation of turgor; (2) the guard cells continue to use K⁺ and are able to limit their intake of Na⁺. The second adaptation is worthy of further exploration because it may provide a means for ‘top down’ control of transpiration and, therefore, of the amount of salt delivered to the shoot. This mechanism may be very important in some of the glandless halophytes, and it could be of particular interest as a potential contributor to the development of salt tolerance in crops.

Key words: Salt tolerance, stomata, transpiration, halophytes, ionic regulation, sodium ions.

INTRODUCTION

There is a wide spectrum of salinity tolerance among higher plant species, and although many halophytes have been studied in great detail, the basic organismal and cellular mechanisms which clearly distinguish them are still obscure. Some non-halophytes do possess a degree of tolerance of low to moderate salt in their rooting environments, but others are killed rapidly at very low external salt concentrations. This, together with other examples of extensive variation may well justify the widespread belief that tolerance is determined by a complex interplay of different structural and physiological factors, but concern has been expressed that there has been insufficient experimental testing of more simple hypotheses (Munns, 1993).

Much attention has been given to mechanisms for intracellular compartmentation of salt, but Cheeseman (1988) cautioned that control is also needed of the total amount of salt actually reaching the leaves because there must be limits to what can be achieved by compartmentation. The bulk of this control must depend on the ability of the roots to exclude salts from the transpiration stream. Nevertheless, salt does reach the leaves via the xylem and, in halophytes, this serves a physiological purpose because its accumulation in the tissues can play a major part in lowering the plant water potential below that of the soil, which itself has been lowered by the presence of salt. Thus the ability of the plant to take up water is maintained. The extent to which Na⁺ contributes to this osmotic adjustment varies, particularly between the dicotyledonous and monocotyledonous halophytes, with the latter group making greater use of K⁺ and sugars than of Na⁺ to achieve the necessary adjustment (Flowers, 1985). It is generally accepted that compartmentation of salts in the cell vacuole is complemented by cytosolic synthesis of organic osmotica which balances the water potential across the vacuolar membrane.

Many non-halophytes respond to the presence of NaCl in the rhizosphere by excluding salt from the shoot, and only when the external concentration has exceeded a tolerable level do appreciable amounts of salt appear in the shoot tissues. If the plant is able to adjust osmotically then this is mainly achieved through synthesis of organic osmotica, which is energetically more expensive than using the readily available NaCl. It is, however, an oversimplification to say that exclusion from the shoot is the prime determinant of salt tolerance in non-halophytes. Alberico and Cramer (1993) found salt tolerance to be poorly correlated with shoot Na⁺ content in cultivars of Zea mays and they suggested that, in this species at least, it is the ability of the plants to maintain lowered cytoplasmic Na⁺ concentrations which determines salt tolerance.

To describe physiological aspects of salt tolerance satisfactorily, it is necessary to have a much better understanding of the range of concentrations of Na⁺ that is acceptable in the cytoplasm, and it is appropriate that this should be a major focus of much current research. In this review we draw attention to another aspect of physiological
control that has received scant attention in halophytes, namely the functioning of stomata. Our own recent research has revealed some unusual characteristics of the ionic relations of the guard cells of a glandless halophyte, Aster tripolium. In some non-halophytes in which the features of guard cells are well studied, sodium ions cause a disruption of the normal regulation of guard cell turgor. This does not occur in A. tripolium, which is clearly important for its survival under saline conditions, but of even greater significance may be the apparent ability of Na\(^+\) per se to exert strong control over stomatal apertures. In this article we discuss the new information in relation to current knowledge of stomatal mechanisms in halophytes, and suggest that some degree of ‘top-down’ control of transpiration, in which the guard cells act as sensors of apoplastic Na\(^+\), may be an additional adaptive feature worthy of exploration in future research.

**The Importance of Transpiration**

Most, and probably all, of the Na\(^+\) delivered from the roots to the shoots is via the xylem stream, although salt can also enter the shoot directly when plants in a tidal zone are immersed in seawater. The evidence for quantitatively significant phloem transport of Na\(^+\) is controversial, but there are few, if any, examples of major contributions to salinity tolerance. Basipetal transport via the phloem has been recorded but it is most common in the most salt sensitive species (Lessani and Marschner, 1978). In contrast, halophytes do not seem to re-translocate Na\(^+\), judging from the small amounts of the ion present in non-transpiring phloem-fed structures such as the ray florets of Aster tripolium L. (Gorham, Hughes and Wyn Jones, 1980). Consequently, the rate of accumulation of salt in the shoots of halophytes will be determined by the rate of transpiration, the concentration of Na\(^+\) in the xylem sap and any excretion processes that may be occurring (e.g. via salt glands and hairs).

Transpiration rates generally tend to decline with increasing rhizospheric salinity in both halophytes and non-halophytes. This might be due to lowered water potentials in the roots, and the transfer of abscisic acid from root to shoot as a signal [cf. the mechanism operating in plants in drying soils (Zhang and Davies, 1991)], but at higher concentrations it could also be the result of inhibition of photosynthesis caused by salt accumulation in the mesophyll, and increasing intercellular CO\(_2\) concentrations which reduce stomatal apertures (Mansfield, Atkinson and Hetherington, 1990). There is evidence that salt accumulation does interfere directly with photosynthesis in non-halophytes (Seemann and Critchley, 1985; Yeo, Caporn and Flowers, 1985), but this is unlikely to occur in halophytes at realistic external salt concentrations (Flanagan and Jeffries, 1989). There is also another potential action of NaCl on transpiration, occurring as a result of the direct inhibition of stomatal opening by apoplastic Na\(^+\) concentration, which has been suggested by recent studies of Aster tripolium (Perera, Mansfield and Malloch, 1994).

Flowers (1985) pointed out that there have been few investigations of the long-term balance of ionic concentrations in individual leaves. In principle, regulation of import of Na\(^+\) via the xylem by regulation of transpiration could be a means of exerting some control over the salt burden in leaves both in the long and short term. Commenting on the need for regulation of the quantities of salt delivered to leaves, Cheeseman (1988) wrote: “Some higher level integrating mechanism must exist, regardless of its effectiveness in producing ‘tolerance’”. We pose the question—could stomatal control of transpiration, based on some means of ‘monitoring’ the salt content of the leaves, make a significant contribution to the required mechanism?

**Sodium Effects on Stomatal Guard Cells (Non-Halophytes)**

Stomatal movements are brought about by changes in the turgor pressure of the guard cells which, in the vast majority of cases examined, result from fluxes of K\(^+\) across the plasma membrane and tonoplast. Chloride ions may be transported alongside K\(^+\), or the necessary anionic balance may be achieved by generation of malate within the guard cells. The first specific suggestion that the osmotic changes behind stomatal movements were the result of transport of K\(^+\) into and out of the guard cells were made nearly 30 years ago (Fujino, 1967; Fischer, 1968), but as early as 1905 Macallum had shown using histochemical staining that the guard cells of tulip accumulated K\(^+\). There had also been a few other studies of the ionic responses of stomata in isolated epidermal strips, and these clearly suggested that several different monovalent cations, in addition to K\(^+\), could support stomatal opening (Imamura, 1943; Iljin, 1957). Iljin (1957) had sufficient confidence in the available data to rank the effectiveness of various cations in promoting stomatal opening—Li\(^+\) > Na\(^+\) > Cs\(^+\) > K\(^+\) > Rb\(^+\). More recent work has not supported such a fixed relationship and it is clear that there are differences between species, and also some dependency on experimental conditions. For example, Humble and Hsiao (1969) observed a very specific requirement for K\(^+\) (mimicked by Rb\(^+\)) in Vicia faba L. when stomata were induced to open in light. Although Na\(^+\), Li\(^+\) and Cs\(^+\) could also support stomatal opening, much higher concentrations were required for maximum effect, and there was also no difference in the degree of opening between light and darkness in the presence of these ions, whilst light greatly enhanced opening in the presence of K\(^+\). There were only small differences in the dose-response of stomatal aperture to K\(^+\), Li\(^+\), Cs\(^+\) and Na\(^+\) in darkness. Willmer and Mansfield (1969) also found that Na\(^+\) and K\(^+\) had similar abilities in supporting stomatal opening in Vicia faba, but Na\(^+\) was more effective than K\(^+\) in supporting stomatal opening in Commelina communis L.

Under normal circumstances Li\(^+\), Rb\(^+\) and Cs\(^+\) are unlikely to occur at physiologically relevant concentrations in plant tissues. This is not, however, true for Na\(^+\) and the neglect of its possible effects on stomatal functioning during research into salinity tolerance is surprising. In halophytes it is likely to be present at relatively high concentrations in the vicinity of the stomata, but perhaps more significant are its possible disruptive effects on stomatal behaviour of non-halophytes.
growing under saline conditions. We are aware of only three studies that have addressed this important issue. Jarvis and Mansfield (1980) using isolated epidermis found that the stomata of *Commelina communis* opened as readily in the presence of NaCl as in KCl (Fig. 1), but they also discovered that thereafter the stomata showed greatly reduced closing responses to darkness, CO$_2$ and abscisic acid (Fig. 2). If this were to occur in a plant growing in salt-polluted soil, there could be serious interference with the control of gas exchange at all times, and even a small degree of water deficit stress would probably be lethal. There is a clear implication that the impact of salt on plant water relations could extend far beyond any effect it has in reducing soil water potential.

Since these data were published 17 years ago, we have only been able to locate two reports of the impact of salt on the functioning of stomata in non-halophytes. Clint (1984) found that guard cells became irreversibly damaged if they were allowed to accumulate excessive amounts of sodium ions, and Thiel and Blatt (1991) monitored the time- and voltage-dependent characteristics of the K$^+$ channels of the guard cell plasma membranes, and found that when Na$^+$ was introduced into the cytoplasm, the outward-rectifying K$^+$ channel current was depressed. A similar blockage by cytoplasmic Na$^+$ has been recognized in animal systems for many years (e.g. Chandler and Meves, 1965). In guard cells, the outward K$^+$ rectifier provides the main route for K$^+$ efflux during stomatal closure. Its inhibition would, therefore, ‘lock open’ the stomata, and Thiel and Blatt (1991) used this to explain the observation made by Jarvis and Mansfield (1980) that when guard cells of *C. communis* had opened in the presence of NaCl their closing responses to ABA, CO$_2$ and darkness were much reduced. Our own recent studies (Robinson, unpubl. res.) have shown that the stomata of some other non-halophytes respond to Na$^+$ in a very similar manner to those of *C. communis*, suggesting that the phenomenon may be widespread.

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**Fig. 1.** The effect of changes in concentration of NaCl and KCl on stomatal opening in detached epidermis of *Commelina communis*, in light and in the absence of CO$_2$. Points represent the means of 90 measurements. Compiled from data of Perera Jayakody (1995).

**Fig. 2.** The effects of light, CO$_2$ and ABA ($10^{-5}$ mol m$^{-3}$) on stomatal opening on detached epidermis of *Commelina communis* in the presence of KCl or NaCl (50 mol m$^{-3}$). Bars represent the means of 90 measurements ± 95% confidence limits. Compiled from data of Jarvis and Mansfield (1980) and Jarvis (1982).
STOMATAL RESPONSES TO SODIUM IN HALOPHYTES

The evidence that the stomata of non-halophytes may be disabled if Na⁺ enters the cytoplasm of the guard cells suggests that halophytes must, as one of their adaptive features, have evolved different stomatal ionic properties. From a theoretical standpoint we might suggest two different ways of overcoming the problem: the guard cells might acquire the ability (1) to use Na⁺ instead of K⁺ as the principal ion determining their changes of turgor, or (2) to exclude Na⁺, enabling K⁺ to retain the principal role. Surprisingly, studies of the ionic relations of halophytic stomata, with particular respect to Na⁺, are rare, but the literature nevertheless provides evidence that both these methods exist, and also that the second of them could make a contribution to the control of salt uptake at the whole-plant level.

Cations and stomatal functioning in halophytes

Eshel, Waisel and Ramati (1974) used X-ray microprobe analysis to measure the relative amounts of Na⁺ and K⁺ within the epidermal and guard cells of Cakile maritima, a halophyte of the seashore. Plants grown in the absence of NaCl contained little Na⁺ (measured as a mean number of counts per minute) in their guard cells, and as expected the K⁺ content was much greater when the stomata were open than when they were closed. On the other hand, when the plants were grown in the presence of 100 mol m⁻³ NaCl, there was much less K⁺ in the guard cells, and little difference between open and closed stomata. Na⁺ appeared to be the major cation within the guard cells of salt-grown plants of C. maritima, and the Na⁺ content increased markedly when the stomata opened. Thus, the guard cells of this species appear to have a facultative ability to use either K⁺ or Na⁺ to support the osmotic changes to drive stomatal movements, depending on the salinity of the rhizosphere in which the plant is situated.

This apparent ability of Na⁺ to substitute for K⁺ in the stomatal mechanism has also been suggested by X-ray microanalysis of the epidermis of Suaeda maritima L. Dum., another halophytic species. In the guard cells of salt-grown S. maritima, Na⁺ was seen to be the major cation, and there were lower concentrations in the guard cells of closed stomata (Flowers et al., 1989). In addition, Na⁺ concentrations appeared to increase in the epidermal cells surrounding closed stomata, a situation analogous to that found with K⁺ in the epidermis of non-halophytes during stomatal movements. In Commelina communis, for example, the surrounding epidermal cells provide a pool of K⁺ for the guard cells (Penny and Bowling, 1974).

In contrast to the situation in C. maritima and S. maritima, X-ray microanalyses have shown that in Aster tripolium there are substantial amounts of K⁺ in the guard cells of salt-grown plants. Although the relative amounts varied depending upon whether the guard cells were on the abaxial or adaxial leaf surface, or whether the analysis was performed on detached epidermis or leaf sections, K⁺ remained the dominant cation in the guard cells, and the Na⁺ K ratio never exceeded 0.13 (Perera, De Silva and Mansfield, 1997). This contrasted markedly with the ratios measured in other leaf cells, which were as high as 2.4 in the epidermal cells adjacent to the stomata (there are no anatomically distinct subsidiary cells in this species) measured in leaf sections. This suggests that the guard cells must have a very effective mechanism for restricting the entry of Na⁺. The distribution of ions in epidermal strips of C. communis was found to be very different (Perera et al., 1997). It proved impossible to grow C. communis with significant amounts of external salinity, and so epidermal strips were treated directly with either 50 mol m⁻³ NaCl or KCl, and the ionic contents were then determined. Even when strips were incubated in NaCl, considerable amounts of K⁺ remained in the epidermal cells, but the guard cells accumulated large amounts of Na⁺ and lost much of their K⁺. Accumulation of Na⁺ by the guard cells of this species is likely to lead to irreversible damage (Clint, 1984). We have found responses of stomata to NaCl that are closely similar to those of C. communis in two other non-halophytes, Aster amellus and Aster subcoeruleus (Perera Jayakody, 1995; Robinson, 1996). It seems likely that the inability of guard cells to exclude Na⁺, the tendency to accumulate it in preference to K⁺, and the subsequent loss of stomatal control of water relations, may contribute significantly to the injury that occurs in non-halophytes under saline conditions.

The ionic responses of guard cells of A. tripolium have also been investigated in isolated epidermal strips, under conditions allowing the responses of functional guard cells to be studied under controlled conditions. Whilst Na⁺ was found to support stomatal opening in isolated epidermal strips from non-halophytes such as C. communis, V. faba (see above), Aster amellus and A. subcoeruleus (Perera Jayakody, 1995; Robinson, 1996) stomatal opening was inhibited by Na⁺ in a concentration-dependent manner in A. tripolium (Fig. 3).

Control of stomatal conductance by sodium ions—a physiological role in Aster tripolium?

Because the transport of salt occurs mainly via the transpiration stream, the regulation of transpiration is an obvious means of controlling the accumulation of salt in the shoot. For this reason the observed response of the stomata of Aster tripolium to Na⁺ concentration is particularly interesting because it provides a mechanism by which regulation of transpiration could be achieved. Aster tripolium lacks any apparent means of removing excess salt from the shoot. Some halophytes possess salt excretory mechanisms such as glands or hairs which actively accumulate salts before releasing them to the exterior (e.g. Spartina sp., Limonium vulgare and Halimione portuloides). For those species which have them, these mechanisms are likely to provide some regulation of the ionic concentrations within the tissues (Flowers, 1985). The possession of such mechanisms is, however, by no means the norm among halophytic species.

It was suggested by Perera et al. (1994) that inhibition of stomatal opening by Na⁺ provides a ‘top-down’ regulatory
mechanism for the control of the salt burden in the shoot, which becomes important when the amount of salt entering the shoot begins to exceed the capacity for compartmentation of the salts in the cell vacuoles. At this point two events are likely to occur. First, the concentration of Na\(^+\) within the apoplast is likely to increase and second, if this is not controlled, accumulation within the cytoplasm will occur and will eventually lead to inhibition of enzyme activity. Because of the small volume of the apoplastic space compared with that of the cell, it can play only a minor role in the accommodation of salt without causing a problem for the regulation of cell water relations (Oertli, 1968; Flowers, Hajibagheri and Yeo, 1991). Flowers and Yeo (1986) pointed out that for a plant transpiring at a rate of 30 cm\(^3\)H\(_2\)O g\(^{-1}\) d. wt d\(^{-1}\), and with a xylem concentration of 10 mol m\(^{-3}\) NaCl and tissues in which the apoplast contributes 1% of the total volume, the protoplasts would have to accumulate at least 99% of the ions delivered if the apoplastic concentration were not to rise faster than that in the protoplast. We have estimated that for A. tripolium the Na\(^+\) concentration in the xylem is around 6 mol m\(^{-3}\) when the external salinity is 100 mol m\(^{-3}\), rising to 12.5 mol m\(^{-3}\) when the external concentration is 300 mol m\(^{-3}\) (Robinson, 1996). These estimates were made under conditions in which transpiration rates ranged from 18.6 to 307 cm\(^3\) g\(^{-1}\) d. wt d\(^{-1}\). However, we do not yet know the distribution of salt between the apoplast and symplast in A. tripolium. It is possible that symplastic accumulation can occur at enhanced rates when necessary, with pinocytosis perhaps playing a role (Kurkova and Balnokin, 1994), making excessive apoplastic build-up a rare event.

If the stomatal responses seen in epidermal strips of A. tripolium were also to occur in vivo, increases in apoplastic Na\(^+\) concentration in the vicinity of the guard cells would inhibit stomatal opening and reduce the amount of Na\(^+\) being delivered. Build-up of Na\(^+\) in the vicinity of the stomata might be anticipated because they are the termini of the pathway for liquid water in the transpiration stream. The relevance of such a mechanism becomes particularly apparent when one considers the fluctuating nature of salinity in a saltmarsh soil (the native habitat of A. tripolium). Plants frequently experience Na\(^+\) concentrations of 480 mol m\(^{-3}\) (i.e. seawater) but they can be exposed to 1000 mol m\(^{-3}\) on a drying saltmarsh at low tide. At the other extreme, precipitation can lower the Na\(^+\) concentration below that of seawater, to a minimum value of around 100 mol m\(^{-3}\) (Flowers, 1985).

The responses of the stomata of A. tripolium to Ca\(^{2+}\) ions in the presence of Na\(^+\) also appear to be important. Whilst Ca\(^{2+}\) in the presence of 50 mol m\(^{-3}\) KCl inhibited opening, in the presence of NaCl there was a partial alleviation of the inhibition of opening caused by Na\(^+\) (Perera, Robinson and Mansfield, 1995). This latter response also seemed to occur in intact plants when leaf conductance was determined by diffusion porometry (Perera et al., 1995).

In view of these interactive effects between Na\(^+\) and Ca\(^{2+}\), it can be argued that there is an alternative explanation of the response of the stomata of A. tripolium to Na\(^+\) concentration, viz. that concentrations of Na\(^+\) similar to those employed in the epidermal strip bioassays by Perera et al. (1994) might have been responsible for Ca\(^{2+}\) displacement from the plasma membranes of the guard cells, which in turn might have led to the efflux of K\(^+\) and a reduction in stomatal aperture. There are several observations which lead us to reject this interpretation and to conclude that the observed response in A. tripolium has physiological validity. There is evidence that the integrity of plasma membranes is more resilient to elevated levels of Na\(^+\) in salt-tolerant than in salt-sensitive species (Marschner and Mix, 1973) and, moreover, the stomata of non-halophytes respond to Na\(^+\) by opening (Fig. 1). Perera et al. (1997) found that when epidermal strips of C. communis were incubated for 3 h in media containing 50 mol m\(^{-3}\) NaCl, the guard cells lost much of their K\(^+\) which was replaced by a considerable amount of Na\(^+\). If a breakdown in membrane selectivity were responsible for the reduced stomatal apertures seen in A. tripolium, then stomatal opening due to the entry of Na\(^+\) into the guard cells would be expected. Reduced apertures with increasing Na\(^+\) concentrations were also observed when there was additional K\(^+\) in the incubation medium (Perera et al., 1994), and we have recently studied the time course of closure in response to Na\(^+\) and found little difference in the initial rate whether epidermis was incubated in the presence or the absence of additional K\(^+\) (Robinson, 1996).

Plasma membrane cation fluxes and Na\(^+\) signalling in halophytes

The foregoing discussion has emphasized the importance of Na\(^+\) in the control of stomatal aperture in halophytes, and has underscored our lack of knowledge with respect to
the fundamental attributes of monovalent cation transport across the plasma membranes of halophyte guard cells. Recent patch clamp studies have compared the electrophysiological properties of guard cells from halophytic and non-halophytic species of Aster with a view to uncovering the ionic basis of the differential opening response to Na+ (A.-A. Véry et al., unpubl. res.).

Interestingly, the plasma membrane of guard cells of the halophyte Aster tripolium exhibits very similar underlying cation transport relationships to those of its non-halophyte counterpart Aster amellus, together with a number of other species that lack salt tolerance. Thus, the principal route of cation entry during stomatal opening appears to be via a cation channel which is highly selective for K+ over Na+ and which is insensitive to addition of Na+ in the external medium. This channel displays the hallmark characteristics of inwardly rectifying K+ channels which have been well characterized in plants, including time-dependent opening in response to negative-going voltages (Hedrich and Schroeder, 1989). Likewise, K+ efflux is mediated in both Aster species by outwardly rectifying K+ channels slowly activating in response to depolarizing potentials which are also highly selective for K+. These channels are sensitive to cytoplasmic Na+, their conductance being increasingly reduced as the membrane polarization becomes more positive.

Sodium ions appear to enter the guard cells of both Aster species through a voltage-independent conductance. Although barely discriminating between Na+ and K+, this pathway is highly cation-selective and is inhibited by extracellular Ca2+. The fundamental difference in the response of the halophyte and the non-halophyte to Na+ arises from the regulation of cation permeability by internal (i.e. cytoplasmic) Na+. In response to elevation of cytoplasmic Na+, the inward rectifying K+ conductance of Aster tripolium—but not that of Aster amellus—is strongly deactivated. Two observations point to an indirect effect of Na+. First, the deactivation is variable, and occurs only after a number of minutes. Second, the deactivation is itself strongly inhibited when cytosolic pH and Ca2+ are strongly buffered. It therefore appears that Aster tripolium possesses a Na+-sensing signal transduction pathway which inhibits K+ uptake, and could therefore evoke stomatal closure by shifting the balance of cation fluxes in favour of K+ loss.

IMPLICATIONS FOR THE PRODUCTION OF CROP SPECIES WITH IMPROVED SALT TOLERANCE

From a recent survey of the literature and of patents, Flowers and Yeo (1995) could list only 11 registrations of new cultivars of crop species possessing useful degrees of salt tolerance, which is in sharp contrast to the number of papers published every year on the subject. They suggested two reasons for the limited success: first, that reduction of yields due to salinization has not yet become a problem of sufficient magnitude for plant breeders to give high priority to the production of new salt-tolerant cultivars; and second, that the limited success of simple breeding programmes relates to the polygenic nature of the salt-tolerance trait. A lack of understanding of this latter point has been prevalent in the past and may underlie the failure of attempts to regenerate plants from cell lines selected for salt resistance at the cellular level (see Dracup, 1991).

The ideas put forward here about the involvement of stomatal mechanisms in salt tolerance/sensitivity are admittedly, in places, speculative, but are based on expanding factual information. Some basic differences in stomatal responses to salt between halophytes and non-halophytes have emerged, and these are associated with fundamental changes in the control of ion transport at the plasma membranes of the guard cells which may prove to be of great adaptive significance. In future it will be important to monitor responses at the sub-cellular level, as well as at whole plant level, in order to ascertain the true significance of the observations made on epidermal strips. This will require clear distinctions to be made between direct ionic and osmotic/hormonal effects on stomatal conductance, and complementary studies to further clarify the specialized features of the guard cells. Because of the apparent polygenic control of salt tolerance, it is important to explore thoroughly every contributory process, and the regulation of transpiration is arguably one of major significance.

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LITERATURE CITED


