Salt tolerance in halophytes

from C. D. Field

IN large areas of the world, the soil is too saline to support economic agriculture and more land becomes non-productive each year because of salt accumulation. So recent research into the ability of halophilic plants to survive in very saline environments has taken on a new importance.

The basis of the salt tolerance of halophilic plants is their ability to maintain and tolerate a high salt concentration in the cell. Since many halophytes show a positive growth response to salt in their environment (although they may also survive in a salt-free environment) it has been argued that as well as participating in the necessary osmotic adjustments, the high ion concentration may also be required by the plant for normal metabolic activity.

One possibility might be that the enzymes of halophilic plants, like those in salt-tolerant bacteria, require high salt concentrations for optimal activity. But this possibility seems to have been disproved by recent work (see Flowers, *Ion Transport in Plant Cells and Tissues,* North Holland; 1975) which shows that *in vitro,* enzymes from halophytes are inhibited by ion concentrations much lower than those expected to occur in the cytoplasm, and very similar to those tolerated by enzymes from non-halophytes. Flowers has recently shown (*Proc. R. Soc. Lond.,* **B273,** 523; 1976) that malate dehydrogenase from the halophyte, *Suaeda maritima,* is activated at electrolyte concentrations similar to those required to activate the enzyme from non-halophytes. All the evidence therefore points to the conclusion that halophyte enzymes are neither particularly salt resistant nor salt requiring.

This leads to the idea that the excess sodium ions must be isolated from the cytoplasm in some way. Indirect evidence from efflux analysis and ion mobilities in tissues of halophytes suggests that sodium ions are retained in the vacuole (Flowers, *op. cit.*) and Jeschke and Stelter (*Planta,* **128,** 107; 1976) have shown that sodium ions are largely excluded from the cytoplasm of the halophyte *Atriplex* and barley, using flameless atomic absorption spectroscopy on thin slices of single roots.

This however raises enormous problems of osmotic imbalance between the cytoplasm and the vacuole, which on this hypothesis would hold most of the salt accumulated in the cell. This osmotic imbalance could only be overcome if the water potential of the cytoplasm could be lowered, so that it will attract water fom the vacuole and remain hydrated. This could theoretically be achieved in various ways. The cytoplasm might have an unusually high water-holding capacity arising from its structure, Donnan equilibria might exist between cytoplasm and vacuole, or a non-toxic osmoticum might accumulate in the cytoplasm. There is little evidence for the first two possibilities, but there is increasing support for the third.

Some years ago Stewart and Lee (*Planta,* **120,** 279; 1974) proposed the amino acid proline as the possible osmoticum. They found that in many halophytes proline accounts for more than 30% of the amino acid pool, whereas it is much less in glycophytes although the level in some species increases in response to salt or water stress. Stewart and Lee also showed that proline concentrations of up to 600 mol m^{-3} do not inhibit enzyme activity *in vitro.*

At a recent International Workshop on transmembrane ionic exchanges in plants (CNRS, Rouen, July 1976) Wyn Jones *et al.* put forward another candidate, the quaternary ammonium compound betaine, for the balancing osmoticum. They demonstrated that the betaine content of the halophytes *Atriplex spongiosa, Spartina* x *townsendii* and *Suaeda monoica* increased with external sodium chloride concentration, and that there was a close correlation between betaine accumulation and an increase in sap osmotic pressure above about 400 osmol m^{-3}. They also found that the *in vitro* activity of malate dehydrogenase was not inhibited by 1 M betaine, and that in the presence of low malate concentrations betaine provided partial protection to the enzyme against potassium chloride and sodium chloride toxicity.

These results suggest that betaine may have a similar role to proline in the cytoplasm of certain halophytes. Flowers has recently confirmed that similar levels of betaine occur in the halophyte *Suaeda maritima.* But in all cases direct experimental demonstration of betaine in the cytoplasm is still needed.

A simplified picture of a typical halophilic plant cell now emerges in which the potassium ion and sodium ion concentrations in the cytoplasm are of the order of 100 mol m^{-3} and 150 mol m^{-3}, whereas the vacuole has corresponding concentrations of 100 mol m^{-3} and 500 mol m^{-3} (Flowers *op. cit.*), and the osmotic balance in the cytoplasm is preserved by proline

Hormones, ducks and sex

from John Krebs

IT is well known that steroid hormones influence sexual and aggressive behaviour in many vertebrates. These established and documented effects are of a rather long term nature, involving changes over developmental, seasonal and similar time periods. Recently, J. Balthazart (*J. Zool.,* **180,** 155; 1976) has suggested that much shorter term changes in behaviour might also be caused by fluctuations in hormone levels. He recorded the daily pattern of behavioural activities in two groups of five male domestic ducks housed in outdoor cages during winter. At the same time he took serial blood samples from each male to measure plasma testosterone.

The most interesting behaviour categories for the present discussion were courtship displays, mating attempts, and aggressive attacks on other males or females (there were two females in each group of males). Courtship and mating activity decreased through the day after an early morning peak, although some of the other activities did not show a similar daily rhythm, so there was not simply an increase in lethargy as the day progressed. In relating these changes to plasma testosterone, Balthazart found that the hormone was at a higher level early in the morning than at other times of day, correlating well with the frequency of sexual behaviour. Further, some of the contrasts between the two groups were associated with hormonal differences. One group showed an increase in both display frequency and hormone levels in the afternoon while the other showed neither, but this second group had a higher level of sexual activity overall and a higher mean level of testosterone.

Behavioural differences between individual males did not relate clearly to hormone levels. There was a very slight tendency for males with higher testosterone levels to be more sexually active, but differences in daily rhythm did not relate to hormonal differences.

Balthazart's results raise an intriguing explanation for a mechanism of short term changes in behavioural activity, but it still has to be shown that the changes in hormone level cause the behavioural changes, rather than the other way round.