Transduction of Turgor Pressure by Cell Membrane Compression

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It is suggested that turgor pressure sensing in plant cells occurs *via* compression of the cell membranes; either at the plasmalemma where a pressure gradient exists, or the tonoplast due to the pressure developed inside the cell. Considerations of electro-mechanical forces in electrical breakdown of cells suggests that significant changes in the thickness of *some regions* of the membrane can indeed occur. It is readily envisaged how such changes in membrane thickness can be coupled to changes in active transport processes.

Introduction

It is well known that osmoregulation and growth processes in plant cells are turgor pressure dependent [1–6]. It has been established that the electrical resistance of the membrane, the membrane potential, ion fluxes and enzyme activity of plant cells are turgor pressure sensitive [5, 7, 8]. However, the mechanism by which the cell senses the turgor pressure has as yet not been determined. The localization of the pressure transduction site(s) in itself also presents a problem. Thus, the pressure *gradient* presumably must be largely confined to the plasmalemma. Difficulties might arise in coupling or regulation of ion transport at the tonoplast to pressure gradients at the plasmalemma, as has been suggested by some authors.

In this communication we wish to present evidence that the cell membrane is a compressible structure and consider the possibility that this may provide the pressure sensing mechanism for the cell which can operate either at the tonoplast or plasmalemma. Compression of the membrane in response to the turgor pressure can be significantly large to feature in the transport properties of the membrane.

Electro-Mechanical Forces in Membranes

Whether significant changes in the thickness of the membrane occur in response to changes in the pressure P, depends of course on the magnitude of the compressive elastic modulus of the membrane. Data on this parameter can be obtained quite readily from an instability condition in the electro-mechanical forces in the membrane as will be shown below [9, 10]. Consider a membrane composed of a homogeneous dielectric material. The membrane separates two ionic solutions and we shall treat it here as a simple capacitor. When a potential difference is applied the membrane will be subjected to a compressive force, P_e, due to the electric field (see Fig. 1). The membrane may also in addition be subjected to a mechanical compressive force, P (such as the turgor pressure in plant cells).

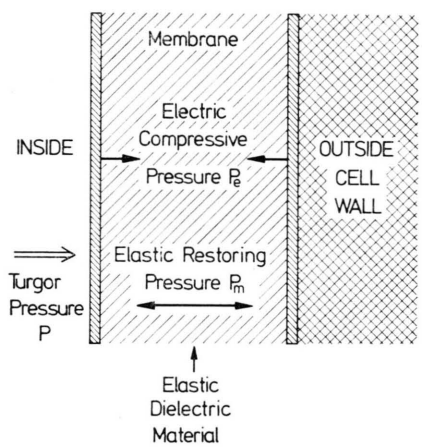

Fig. 1. A schematic representation of the cell membrane. The membrane dielectric is here assumed to be elastic. The membrane acts as a capacitor and the electrical p.d. across the membrane creates a pressure, P_e, tending to compress the membrane. Similarly the turgor pressure, P, will also lead to a compression. These compressive processes are counterbalanced, at equilibrium, by the elastic restoring forces, P_m, generated in the membrane.

For dimensional stability these compressive stresses must be counterbalanced by a mechanical re-

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storing force, P_m, arising from the molecular stress induced in the system. At equilibrium therefore,

$$P + P_e + P_m = 0 . \quad (1)$$

The compressive stress, P_e, due to the potential difference is given by:

$$P_e = \frac{\varepsilon \varepsilon_0 V^2}{2 l^2} \quad (2)$$

where ε is the dielectric constant, ε_0 is the permittivity of free space, V the membrane p.d., l the stressed thickness of the membrane. For a perfectly elastic material the restoring force, P_m, due to a decrease in membrane thickness is given by:

$$P_m = - Y_m \ln \frac{l_0}{l} . \quad (3)$$

Here Y_m is the elastic compressive modules for strains transverse to the plane of the membrane, l_0 the unstressed thickness of the membrane.

For electro-mechanical equilibrium we obtain, therefore, from Eqns (1 – 3):

$$P + \frac{\varepsilon \varepsilon_0 V^2}{2 l^2} = Y_m \ln \frac{l_0}{l} . \quad (4)$$

When the stressed thickness, l, of the membrane is sufficiently small compared with the unstressed thickness, l_0, the membrane can become dimensionally instable. This comes about because the mechanical restoring force, P_m, given by Eqn (3) for a sufficiently small value of l increases more slowly than the compressive force due to the membrane potential given by Eqn (2) and the pressure P (which is independent of l). The membrane thickness can be taken to this critical thickness by applying a sufficiently large membrane p.d. When the critical condition is reached electrical breakdown of the membrane occurs [9–13]. The critical potential, V_c, required to achieve breakdown then can be used to calculate the elastic modulus of the membrane. Thus for instance at a given (turgor) pressure it is readily shown that the elastic modulus is given by:

$$Y_m = \frac{\varepsilon \varepsilon_0}{0.368 l_0^2} V_c^2 .$$

The critical breakdown potentials are in the range of 0.5 – 2.0 V depending on species and physiological condition [9, 12, 13].

The elastic compressive modulus of the cell membrane of various species of plant and animal cells calculated from the breakdown potentials is then of the order of $1.0 - 10 \times 10^6$ Nm^{-2} (10 – 100 bar) [9, 10, 12–14].

These values refer to the breakdown region. In other membrane regions, such as those associated with active transport, the elastic modulus might conceivably be lower. Nevertheless we have at least established the order of magnitude of the moduli of some of the membrane regions. That these values of the elastic moduli are sufficiently small to significantly affect the membrane under the influence of normal turgor pressure is evident from Fig. 2. Here

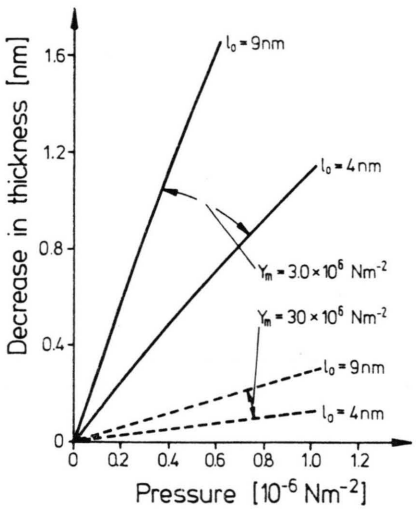

Fig. 2. The calculated changes in membrane thickness in response to changes in turgor pressure in the range of $0 - 1.0 \cdot 10^6$ Nm^{-2} (0 – 10 bar), for values of the elastic modulus $Y_m = 3$ and $30 \cdot 10^6$ Nm^{-2} (30 to 300 bar) and for unstressed thicknesses of the membrane (when $P = 0$) of 4 and 9 nm. The values of Y_m deducted from dielectric breakdown measurements are of $3 \cdot 10^6$ Nm^{-2} (30 bar). It is clear, therefore, that significant changes in the membrane thickness can then result from small changes in the turgor pressure.

the calculated *changes* in membrane thickness are plotted as a function of turgor pressure for several values of elastic modulus, Y_m and the initial unstressed membrane thickness l_0. Evidence that the membrane thickness does indeed respond to the turgor pressure has come from direct measurements of the dependence of the electrical breakdown potential on turgor pressure in *Valonia* [13, 15]. Such measurements, which allow an independent estimate to be made of the transverse elastic modulus, are in agreement with the values calculated from the breakdown mechanism itself [13, 15]. Changes in the thickness of the tonoplast would come about in exactly the same manner as for the plasmalemma; a direct compres-

sion due to the local (turgor) pressure. Thus this pressure transduction mechanism could also operate in the tonoplast. Changes in the thickness of the cell membrane can also result from strains induced by stretching of the cell wall in response to turgor. This would depend on a close coupling of the strains in the cell wall and the cell membrane.

Regulation of cell sap osmolarity and turgor pressure occurs presumably *via* control of active (and passive) transport or other chemical processes in the membrane [2, 4, 5, 7].

It is not difficult to envisage how such processes may be influenced by changes in the thickness of the cell membrane. As outlined above, the membrane thickness will be a function of both the turgor pressure as well as the membrane potential. If the field in the membrane is not uniform, that is in some regions there is a more intense field than in other regions then the osmoregulating mechanism here proposed could be sensitive also to changes in the physiological range in the membrane potential. Hence also the osmoregulation would become selective and sensitive to the concentration of different ions (*i. e.* not only to the total osmotic pressure of the external solution). Some evidence that this is indeed the case has been given by Zimmermann and Steudle [4] for cells of *Chaetomorpha linium*. In this species, for instance, it was found that an increase in external K^+ concentration (which should depolarise the plasmalemma potential) can compensate (and sometimes even over-compensate) for a decrease in the total external osmolarity [8].

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