

10 Electrogenic Pumps

ROGER M. SPANSWICK

10.1 Introduction

The electrical properties of plant cell membranes are quite diverse, reflecting the wide range of environmental conditions to which plant cells are exposed. However, it appears that electrogenic pumps almost always make important contributions to the magnitude of the membrane potential and, in some cases, the membrane conductance (Higinbotham 1973; Spanswick 1981).

Early studies of membrane potentials using intracellular electrodes were summarized by Blinks (1949). Due to technical limitations, the early work involved the use of large freshwater or marine algal cells such as *Valonia*, and it was not until the development of modern microelectrode techniques and electronics that the methods became more reliable, beginning in the late 1950s. Initial approaches to the problem of accounting for the magnitudes of the membrane potential and conductance and their response to changes in external ion concentrations were influenced strongly by the success of animal physiologists in making the simplifying assumption that the gradients of ion concentrations across the plasma membrane were established by neutral ion pumps, i.e. pumps that would not generate a current. It was also assumed that the electrical properties of the membrane were determined entirely by passive diffusion of the ions across the membrane down the gradient for each ion that resulted from its concentration gradient and the common electrical potential gradient, summed as the electrochemical potential gradient. The assumption of a constant electric potential gradient (electric field) within the membrane, together with a constant partition coefficient for an ion at both surfaces of the membrane, makes it possible to integrate the diffusion equations across the membrane and yields an equation for the net passive flux, J . The flux, J_K , for potassium, as an example, is:

$$J_K = -P_K \left(\frac{FE}{RT} \right) \frac{\{[K_o^+] - [K_i^+] \exp(FE/RT)\}}{\{1 - \exp(FE/RT)\}} \quad (10.1)$$

where P_K is the permeability coefficient, E is the difference in electrical potential across the membrane (the membrane potential), $[K_o^+]$ and $[K_i^+]$ are the

Department of Biological and Environmental Engineering, Riley-Robb Hall, Cornell University, Ithaca NY 14853-5701, USA (e-mail: rms6@cornell.edu)

Plant Electrophysiology – Theory & Methods (ed. by Volkov)
© Springer-Verlag Berlin Heidelberg 2006

external and internal potassium concentrations, respectively, F is the faraday and R and T have their usual meanings. The further assumption of a steady state, or specifically that there is no net charge accumulation in the cell, means that the net currents carried by the individual ions must sum to zero. It leads to the equation, usually referred to as the Goldman–Hodgkin–Katz (or GHK) equation (Goldman 1943; Hodgkin and Katz 1949), which, assuming that sodium, potassium and chloride are the only ions transported, has the form:

$$E = \left(\frac{RT}{F} \right) \ln \frac{P_K [K_o^+] + P_{Na} [Na_o^+] + P_{Cl} [Cl_i^-]}{P_K [K_i^+] + P_{Na} [Na_i^+] + P_{Cl} [Cl_o^-]} \quad (10.2)$$

[See Nobel (2005) for a detailed derivation of this equation.]

It is also possible to find an expression for the conductance in terms of the concentrations and permeability coefficients by first applying the condition:

$$\sum z_j F J_j = I, \quad (10.3)$$

where I is the applied current, z_j is the valence of the ion j , and $\sum z_j F J_j$ is the sum of the currents due to the fluxes of the individual ions. Differentiating, to obtain dI/dE , gives the conductance:

$$G_m = \left[\frac{F^3 E}{(RT)^2} \right] \left[\frac{wy}{w - y} \right] \quad (10.4)$$

in the limit $I \rightarrow 0$, where G_m ($S.m^{-2}$) is the specific conductance of the membrane, $w = P_K [K_o^+] + P_{Na} [Na_o^+] + P_{Cl} [Cl_i^-]$ and $y = P_K [K_i^+] + P_{Na} [Na_i^+] + P_{Cl} [Cl_o^-]$. This expression was also derived by Hodgkin and Katz (1949).

Equations 10.1, 10.2 and 10.4 provide the basis for determining whether the electrical properties of the membrane can be accounted for simply by passive diffusion of the ions. The permeability coefficients are defined by Eq. (10.1), or partial equations for the unidirectional fluxes derived from it. Since the membrane potential appears in all the equations, they are not independent. However, if the assumption of passive ion diffusion is valid, the equations should give consistent results. They can, of course, be extended to include other ions that have significant fluxes across the membrane.

The results of early attempts to apply this approach to plant cells were presented clearly by Dainty (1962). Even at that stage, problems were becoming evident. However, the approach does provide a sound quantitative theoretical basis on which to proceed. Thus, permeability coefficients could be calculated from the passive components of the major ion fluxes and used with concentration data to make predictions about the magnitude of the membrane potential and conductance or the response to changes in external ion concentrations.