16 Electrophysiology of Turgor Regulation in Charophyte Cells

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16.1 Turgor regulation

16.1.1 What is turgor pressure?

Turgor pressure is the difference in hydrostatic pressure between the inside and outside of a plant cell. A positive turgor pressure is generated when an osmotic gradient draws water into the cell, but cell expansion is limited by the ability of the cell wall to expand. The pressure that results is a function of the elastic modulus of the cell wall:

$$dP = \varepsilon * (dV/V) \tag{16.1}$$

[See Nobel (1974) for a discussion of water relations in plants, and Findlay (2001) for a recent review of water movement and turgor regulation.] A positive pressure is generally seen as a good thing for plants, particularly by those who work with terrestrial plants. Turgor drives the expansion growth of walled cells. It has a primary responsibility for generating form in non-woody tissues, as the positive pressure inflates the cell, constrained by the often asymmetrically strengthened cell wall. Loss of turgor is considered a bad thing, as environmental factors that reduce turgor cause damage to the plant and loss of agricultural yield (Boyer 1982; Bartels and Nelson 1994). This can be due to a number of factors, such as the inability of cells to grow, of roots to penetrate through the soil, of leaves to expand to optimize photon capture, etc. Turgor is lost when water is withdrawn; shrinkage of the cell results in loss of turgor, again determined by the volumetric elastic modulus (ε; Eq. 16.1). Water is withdrawn from the cell when the water potential outside the cell becomes lower than that inside the cell; this is referred to as hypertonic stress. This term is preferable to the term "hyperosmotic stress", since osmotic pressure is not the only determinant of water movement. Water potential, defined as the chemical potential of water divided by the partial molar volume of water, is affected by a number of different factors, such as hydrostatic pressure, dissolved solutes (osmotic pressure), and the presence of surfaces (matric potential, capillary force, or colloid osmotic pressure).

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Those working on aquatic plants, however, particularly marine plants, need to keep in mind that an increase in turgor has greater potential danger than a decrease. A decrease in turgor is often reversible and non-lethal, particularly if it is small and transient enough that plasmodesmata are not disrupted or cytoplasm markedly dehydrated. An increase in turgor results from an influx of water due to hypotonic stress. (Note that in plant cells, the medium is typically hypo-osmotic even when it is isotonic, because of the effect of turgor on the cells' water potential. "In this case the term 'hypo-osmotic'" to describe the stress is particularly misleading.) Turgor that is sufficient to exceed the mechanical strength of the cell wall results in rupture, which is irreversible and inevitably fatal. Aquatic plants adapted to high salinity often respond to hypotonic stress more rapidly than to hypertonic stress (Bisson and Kirst 1980b; Hoffmann and Bisson 1990; Stento et al. 2000).

16.1.2 How do plant cells regulate turgor?

In order to regulate its turgor in response to environmental challenges, a cell must first be able to determine when its turgor has been perturbed. The mechanism by which a cell measures its turgor is not known in any case. Numerous hypotheses have been proposed (Coster and Zimmermann 1976; Gutknecht et al. 1978; Pickard and Ding 1992, 1993; Bisson and Kirst 1995; Heidecker et al. 1999; Shepherd et al. 2002; Kacperska 2004). They generally invoke physical differences that occur as a result of pressure on or differential pressure across the membrane. This might include proximity between elements of the membrane and cell wall, curvature of the membrane globally or locally, compression of the membrane, and tension within the membrane. Communication of these changes to the cell may occur by alteration in the activity of membrane proteins, particularly ion transporters, and hence may have electrophysiological consequences. For instance, stretch-activated or -inactivated channels within the membrane could change membrane conductance (G) and electrical potential difference across the membrane (PD). These channels themselves could admit calcium into the cytoplasm, or the alteration of PD could activate calcium channels. Calcium could alter the activity of various transporters or enzymes directly or indirectly through the activation of various signal transduction factors. In order to affect turgor, these changes need to result in an alteration of cytoplasmic osmotic pressure that reverses the movement of water and restores the desired turgor. If these processes involve the transport of charged species, they are likely to have electrophysiological consequences.

16.1.3 Other consequences of turgor stress

Survival of osmotic stress involves more than regulating turgor. For instance, if rapid turgor regulation results in a disruption of normal ion ratios, these may need to be restored over the long term, or ionic solutes replaced with