Physiological Dynamics in Animals & Plants – Lecture 11 – Signal transduction in guard cells

I. Guard cells regulate the dimensions of stomata, and thereby regulate rates of transpiration and photosynthesis in higher land plants.

II. Guard cells change shape through changes in their turgor pressure; these changes in shape cause each stoma to open or close.

III. Guard cells change shape in response a variety of environmental signals, including light (intensity and color), intercellular concentrations of leaf carbon dioxide, plant hormones like abscisic acid (ABA), humidity, and pollutants (e.g., ozone).

   A. Stomata open in response to increasing light intensity and are particularly sensitive to blue light.

   B. Stomata close when treated with ABA.

   C. Stomata open in response to decreased intercellular concentrations of carbon dioxide in the leaf (c_i) and close in response to increased carbon dioxide concentrations.

   D. As in other cells, each of these signals must be transduced through a signal transduction pathway.

      1. Stomata open through a chemiosmotic mechanism.

IV. Stomatal opening requires activation of a plasma membrane proton-translocating ATPase (proton pump) which is fueled by ATP.

   A. The pump can be activated by: a) low intensities of blue light applied over a red light background; b) reduced concentrations of carbon dioxide (under red light); c) the plant hormone, auxin; or d) the fungal toxin, fusicoccin

   B. Calcium ions inhibit pump activity.

C. Activation of the proton pump results in transient hyper-polarization of the plasma membrane (inside becomes more negative relative to outside).

1. Hyperpolarization changes the membrane electric potential so that inward-rectifying voltage-gated potassium ion channels open and potassium ions enter the cell along the electrochemical gradient.

a. Potassium ion accumulation is accompanied by uptake of chloride ion and synthesis of malic acid (malate) in guard cells.

2. As the membrane potential changes to be less negative on the inside initially, outward-rectifying, voltage-gated potassium ion channels close as do outward-rectifying, voltage-gated anion channels for chloride ion and malate.

3. Water goes where solutes accumulate, increasing guard cell turgor and causing guard cells to change shape.

4. Sucrose replaces potassium ion at mid-day as the guard cell osmoticum – the mechanism is unknown.

V. Stomata open in response to light and lowered concentrations of carbon dioxide.

A. The guard cell proton pump is activated by very low intensities of blue light.

1. Evidence was first obtained by patch-clamping guard cell protoplasts.

2. Two photoreceptors have been proposed: the carotenoid, zeaxanthin, and the flavoprotein, phototropin.

3. The components of the blue light signal transduction pathway are not fully known, but probably include –

calmodulin

a serine/threonine kinase (MLCK equivalent)

a 14-3-3 protein that binds to the proton pump in the final activation step in the pathway.

B. The guard cell proton pump is activated by reduced concentrations of carbon dioxide.

1. The response must be measured under red light.

2. The response is inhibited by sodium orthovanadate, an inhibitor of the plasma membrane proton pump of plant cells.

3. The response requires photosynthetic electron transport.

4. Potassium accumulates in guard cells during the response.

5. The response in eliminated by calmodulin antagonists and by inhibitors of serine/threonine kinases, suggesting that the signal transduction pathway shares some components of the blue light signal transduction pathway.

VI. Stomata close in response to elevated carbon dioxide and ABA; the mechanisms are under investigation.

A. In both closing responses, calcium (either free concentrations or oscillations in concentrations) is implicated, but calcium is not the sole regulator of stomatal closure for either signal.

B. Little is know about the mechanism of stomatal closure induced by elevated carbon dioxide, but ABA-induced stomatal closure is under intense investigation.

1. Both extracellular and intracellular ABA receptors may exist, but none has been isolated.

2. ABA induces closure by causing massive efflux of potassium ions and anions from guard cells caused by ABA-induced depolarization of the plasma membrane.

   a. Depolarization is accompanied by an increase in cytosolic calcium ion contents – calcium enters guard cells through channels and/or is released from internal stores.

      1. Stomata close when injected with IP_3.

      2. ABA can induce IP_3 production by guard cells.

   b. Potassium ion efflux channels open slowly, and so the effect of ABA must be sustained long enough to cause them to open.

      1. This long-term depolarization involves opening of “slow” anion channels on the plasma membrane.

3. ABA also increases cytosolic pH which activates potassium ion efflux channels on the plasma membrane.

4. SUMMARY: ABA causes increases in cytosolic calcium during which a transient depolarization of the plasma membrane takes place. Transient depolarization is followed by a slower, continued depolarization caused by the opening of slow anion channels in the plasma membrane. When the membrane reaches the right potential and the cytosol reaches the right pH, potassium ion efflux channels open and previously open potassium ion influx channels close. Increased cytosolic pH and increased concentrations of calcium ion in the cytosol decrease the activity of the plasma membrane proton pump.

5. Recent data implicate reactive oxygen species such as hydrogen peroxide and sphinogsine-1-phoshpate as components of ABA signal transduction pathways in guard cells.

6 ABA can activate a protein kinase (ABA-dependent protein kinase = AAPK) that can cause stomatal closure through a calcium-independent pathway yet to be elucidated.

7. Guard cells have redundancy of signal transduction pathways for ABA.

VII. Alternating metabolism of internally-produced guard cell ABA and exposure of guard cells to ABA in the transpiration stream may explain diurnal patterns of stomatal opening and closing.