

STOMATAL DYNAMICS

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Stomatal pores are microscopic openings in the leaf surface which permit the gas exchange of CO_2 and water vapor between the leaf interior and the environment. CO_2 is used by the plant in photosynthesis. When the stomatal pore is open, however, not only does CO_2 enter the leaf but water vapor also diffuses out of the leaf into the atmosphere. Water loss is undesirable, especially in times of drought. Stomata therefore have the dual task of permitting sufficient entry of CO_2 while avoiding excessive water loss. A clearer understanding of stomatal dynamics is expected to lead to application in crop production models.

The stomatal pore is bounded by two specialized guard cells which act as a valve in regulating pore size [1], see Fig. 1. In addition to transient responses, stomata have been observed to oscillate, even under constant environmental conditions. Experiments have revealed two oscillations, one of about 10-50 minute period associated with an hydraulic feedback loop, and another of about 2-5 minute period associated with a CO_2 feedback loop [2].

Delwiche and Cooke [3] have modelled the hydropassive aspects of stomatal dynamics, but did not include the CO_2 loop. The specific objective of the present study is to extend this previous work by including the effects of the CO_2 feedback loop.

The model is based on the schematic diagram of Fig. 2. It takes the form of an autonomous system of three coupled first order ordinary differential equations, derived from a consideration of liquid and gas fluxes between guard cells, neighboring subsidiary cells and intercellular air spaces.

The CO_2 oscillation may be described in words as follows: CO_2 entering the stomatal pore by diffusion is absorbed by the wet cell walls of the guard cells. Dissolved CO_2 diffuses through the cell liquid to carboxylation sites where malic acid is produced. The H^+ ions of the dissociated malic acid are actively pumped across the guard cell membrane, increasing the negative electrical charge inside the guard cell. In response to this, K^+ ions passively diffuse into the guard cell from the neighboring subsidiary cells. The osmotic content of the guard cell is now increased causing water to flow passively into the guard cell. The resulting increase in hydrostatic pressure (turgor) causes the stomatal pore width to increase. This continues until the H^+ pump reaches its maximum capacity, after which the H^+ ions begin to accumulate inside the guard cell and the resulting pH change forces the K^+ ions to passively diffuse out of the guard cell. The water follows the K^+ ion transport and the guard cell turgor drops; causing the stomatal pore width to decrease.

This CO_2 oscillation is to be contrasted to the hydropassive oscillation studied previously [3]. The hydropassive oscillation may be described in words as follows: Water vapor evaporating from the wet mesophyll cell walls diffuses through the stomatal pore to the leaf exterior. This water is replaced both by a flux brought to the leaf mesophyll from the roots via the vascular system, as well as by water diffusing passively from the guard cells to the mesophyll cells. The resulting decrease in turgor in the guard cells causes the stomatal pore width to decrease. A smaller pore width slows the rate of evaporation and causes water to accumulate in the mesophyll cells. In response to this accumulation, water diffuses back to the guard cells, increasing their turgor and increasing the pore width.

The current model includes both the CO_2 and the hydropassive loops, as well as a hydroactive feedback loop (Fig. 2). The hydroactive loop is modeled by requiring that the H^+ pump capacity in the guard cell be dependent upon the water potential in the mesophyll cells. This models the hypothesis [4] that abscisic acid is produced in the mesophyll under water stress, and upon arriving at the guard cells, causes solute loss.

Our mathematical model predicts that the system exhibits a limit cycle in three dimensional state space. The resulting oscillation is shown to possess (1) a hydraulically-based oscillation with a period of about 20 minutes and (2) a CO_2 -based oscillation with a period of about 2 minutes. The CO_2 -based oscillation is superimposed upon the water-based oscillation (Figs. 3,4).

By selecting parameters such that the water vapor concentration is identical inside and outside the leaf, the water vapor flux and hence the hydraulic-based oscillation can be suppressed. The result is that the CO_2 -based oscillation can be isolated (Fig. 5). Note that the CO_2 oscillation occurs only when the stomatal pore is nearly closed.

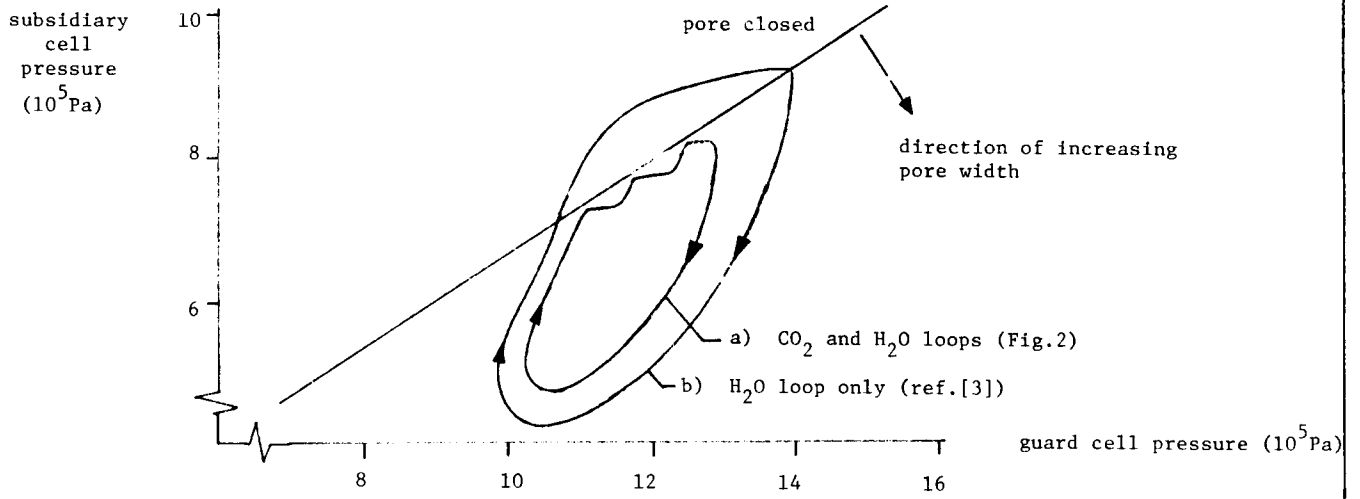


Fig. 3. Limit cycles in phase plane for a) model of Fig.2, and b) simplified model of ref.[3].

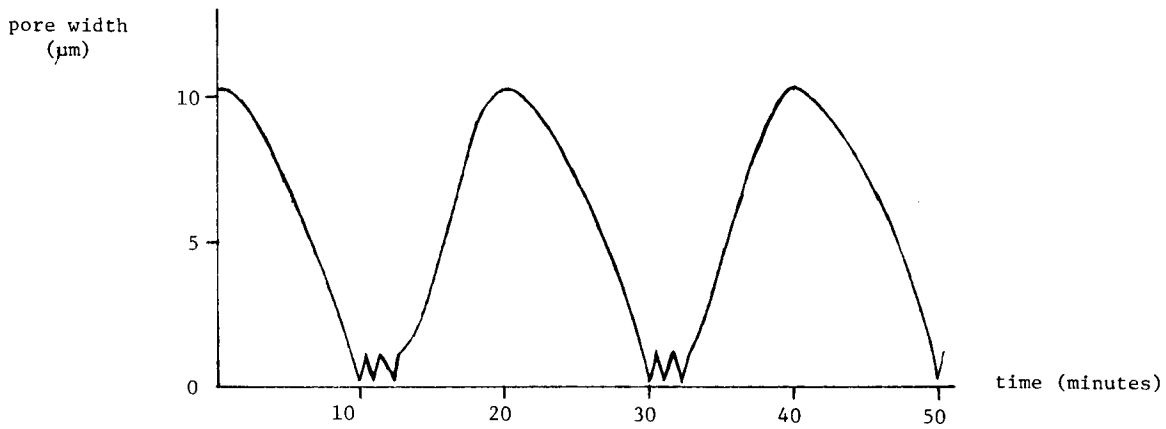


Fig. 4. Pore width versus time for limit cycle of model of Fig.2; cf. Fig.3.

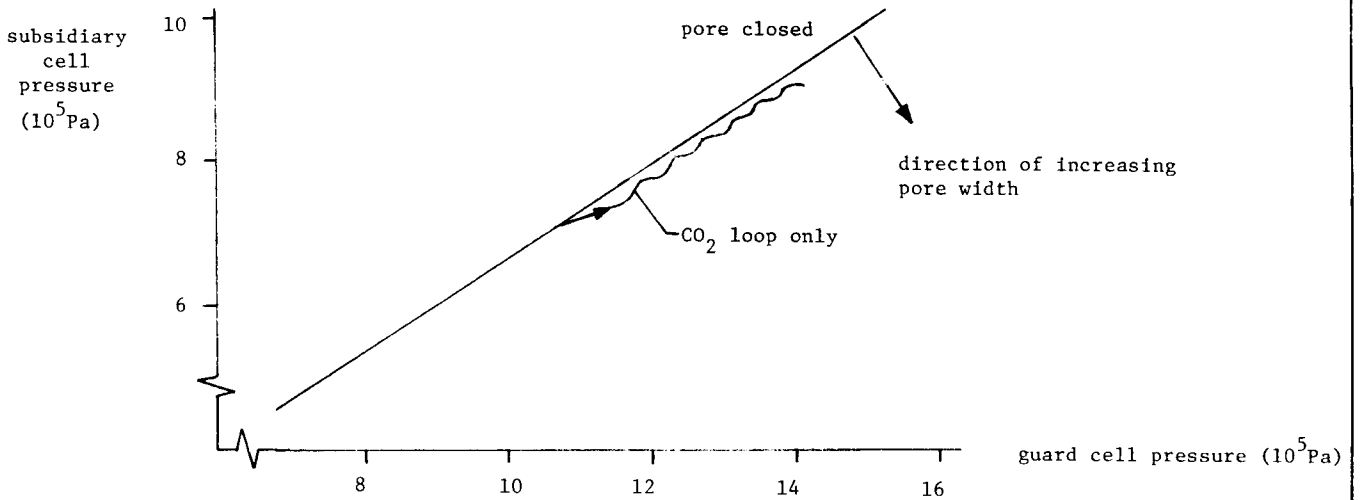


Fig. 5. Phase plane oscillation for model of Fig.2, but without hydraulic feedback loops.

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