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Generalized hydromechanical model for stomatal responses to hydraulic perturbations

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AUTHOR-HIGHLIGHTS

- We model the 'soil–plant–air' system describing stomatal responses to water.
- Our model is described by the dynamics of water and osmolytes transport in plant.
- The turgor pressure of a cell is taken to be a power function of its volume.
- Both stationary and nonstationary results agree qualitatively with the experimental data.
- Our model can be extended further to describe stomatal responses to several environmental factors.

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ABSTRACT

Stomata respond in a common pattern to various hydraulic perturbations on any part of the 'soil–plant–air' system: initial transient 'wrong-way' responses and final stationary 'right-way' responses. In order to describe this pattern on the basis of statistical physics, we propose a simple model where turgor pressure of a cell is taken to be a power function of its volume, and obtain results in qualitative agreement with experimental data for responses to a variety of hydraulic perturbations: Firstly, stationary stomatal conductance as a function of the vapor pressure deficit divides into three regimes characterized by sensitivities of the stomatal conductance and the transpiration rate with respect to vapor pressure deficit; secondly, for every hydraulic perturbation, the initial transient 'wrong-way' responses always appear; thirdly, on condition that water is supplied insufficiently, stomatal oscillations are often observed; finally, stomatal responses following leaf excision exhibit, after the initial transient wrong-way responses, slow relaxation to stomatal closing. In particular, comparison of areoles having different numbers of stomata demonstrates that areoles with small numbers of stomata tend to provoke lack of water in the soil as well as in the plant. In addition, our model also describes well dependence of the stomatal conductance on temperature. It may be extended further to describe stomatal responses to other environmental factors such as carbon dioxide, light, and temperature.

1. Introduction

Stomata respond to various environmental factors, e.g., water, temperature, carbon dioxide, light, and so on. Above all, water is the most important factor to plants due to material transport and cooling. In comparison with studies on stomatal responses to temperature, carbon dioxide, or light, stomatal responses to water have been studied for a longer time. Although the latter studies have produced experimentally and theoretically good results, the key mechanism of the stomatal responses still remains unknown and no model describes well both stationary and non-stationary responses.

It has been found that stomatal conductance at stationarity divides into three regimes of high, medium and low humidity, characterized by the sensitivities of the stomatal conductance and the transpiration rate with respect to vapor pressure deficit (Monteith, 1995). In the high- and medium-humidity regimes, the transpiration rate increases as the humidity decreases. Entering the low-humidity regime, however, the transpiration rate gets reduced. Explanations as to why the transpiration rate reduces in the low-humidity regime include xylem cavitation (Oren et al., 1999; Buckley and Mott, 2002; Dewar, 2002) [for general discussion on xylem cavitation, see Jones and Sutherland, 1991; Sperry et al., 1993, and Sperry, 2000], cuticular transpiration (Farquhar, 1978), patchy stomatal closure (Mott and Parkhurst, 1991), and abscisic acid (Mott, 1995; Zhang and Outlaw, 2001a, 2001b). Unfortunately, which is the key factor still remains to be a matter of debate.

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To an abrupt change in the vapor pressure deficit (equivalently, change in humidity), initial stomatal responses are opposite to the final responses; these phenomena are called the initial transient wrong-way responses. It is in consensus that these responses are caused by mechanical advantages of epidermis (DeMichele and Sharpe, 1973; Wu et al., 1985; Spence et al., 1986; Klein et al., 1996). After initial transient wrong-way response, guard cells, however, must overcome the mechanical advantages of epidermis in order to produce final stationary right-way response. The draw-down model (Raschke, 1970; Lange et al., 1971) and the osmotic regulation model (Meidner, 1986; Grantz, 1990) were established as the overcoming mechanism, which was theoretically analyzed by Buckley and Mott (2002). Still, if the key factor – whatever it is – in producing the wrong-way response overwhelms the overcoming mechanism, then the wrong-way response appears again and then the right-way response does and so on, giving rise to oscillations of stomata. Indeed, under poor conditions of water, stomata often oscillate (Cowan, 1972; Farquhar and Cowan, 1974; Rand et al., 1981; Haefner et al., 1997; Jarvis et al., 1999; Wang et al., 2001). There are two suggestions for the mechanism to induce oscillations: one is the osmotic regulation of guard cells and the other is the stomatal patchiness, albeit the origin of stomatal patchiness is not clear.

In response to excise a leaf from the plant, stomata open and then close. Observation of this behavior, called the 'Iwanoff effect', dates back to Darwin in 1898. In spite of its long history, there are still few models describing plausibly such stomatal responses to the leaf excision.

Even though various models have already been suggested to explain the above phenomena, none of them could explain all the phenomena. For instance, the model of Haefner et al. (1997), in which an areole on a leaf is viewed as a square lattice and hydraulic interactions between neighboring sites on the lattice are included, exhibits only one of the three regimes at stationarity and fails to reproduce the stomatal responses following leaf excision.

The purpose of this paper is to establish a model for stomatal stationary and non-stationary responses to various hydraulic perturbations. Specifically, we propose a model which describes accurately the above phenomena and is as simple as possible in the spirit of Occam's razor.

2. Model and method

2.1. Model description

This study is devoted to modeling responses of stomatal conductance (or equivalently, stomatal aperture) only to hydraulic perturbations. Accordingly, various environmental factors affecting the stomatal conductance are disregarded except water. For example, carbon dioxide, light intensity, or temperature are assumed to remain constant during stomatal responses to hydraulic perturbations, so that their effects do not come into action. We thus focus on how much the stomatal conductance varies, rather than how high it is.

In describing stomatal responses to various hydraulic perturbations, it is essential to include the water transport system in the plant, consisting of the root, xylem in the trunk, xylem in the leaf veins, and several kinds of cells in leaves. However, the root and the xylem in leaf veins are not specified explicitly in the model because we are not concerned with their water potentials or water contents; rather, they are merged into the xylem in the trunk and thus the word 'xylem' in this paper stands for the integrated system of the root, xylem in the trunk, and xylem in leaf veins. In consequence, the xylem plays the role of a passage through which water is transported from soil to epidermal cells neighboring with the leaf veins.

To make the model hydromechanically concrete, we regard water as an incompressible liquid in view of the extremely small compressibility (of the order 10^{-4} MPa), and adopt the continuity equation describing water flow.

2.2. Water flow pathway

While it is apparent that water is absorbed into a plant via its root and water vapor is transpired from its leaves to the ambient air, the exact pathway of water transport from xylem to the evaporating sites still remains unknown, thus making it necessary to choose one of the several candidates for the pathway. Among them, we consider the water flow pathway as illustrated in Fig. 1 [similar to design 2 in Zwieniecki et al., 2007]. This pathway has two characteristics: first, direct water flow from xylem to mesophylls is blockaded and second, direct water flow between guard cells and mesophylls is also inhibited. In fact, allowing them turns out not to give significantly different results. On the other hand, the water flow from the epidermal cell to the mesophyll is allowed (Zwieniecki et al., 2007) in accord with the good evidence that a mesophyll cell interacts hydraulically with adjacent epidermal cells (Nonami and Schulze, 1989). In addition, the guard cell is in hydraulic contact only with the epidermal cell.

In the model, while it is considered that evaporation into a substomatal cavity occurs mainly on the surface of the mesophyll and the guard cell wall also contributes to it, the evaporation from an epidermal cell to a substomatal cavity is not taken into account and only its cuticular transpiration to the ambient air is considered.

2.3. Stomatal region and lattice model

When one draws imaginary middle lines between every pair of neighboring stomata as the Voronoi partition in mathematics or the Wigner–Seitz cell in solid state physics, the leaf is divided into as many regions as there are stomata: each region contains one stoma, one substomatal cavity, a pair of guard cells, a pair of subsidiary cells, a few epidermal cells and mesophylls, and so on. We call it a 'stomatal region' (corresponding to a unit cell on a lattice). Fig. 2 illustrates the $L \times L$ square lattice of an areole surrounded by leaf veins; each site on the lattice represents one stomatal region. At a site (i.e., in a stomatal region), epidermal cells interact hydraulically with guard cells and mesophylls, whereas the second characteristic of the water flow pathway does not allow the guard cells to interact hydraulically with the mesophylls. In addition, the interactions between neighbouring sites are achieved only through the epidermal cells: While an epidermal cell at a site interacts hydraulically with the epidermal cells at the four nearest neighbouring sites (above, below, left, and right in Fig. 2), the mesophyll does not interact with one in the neighbouring site.

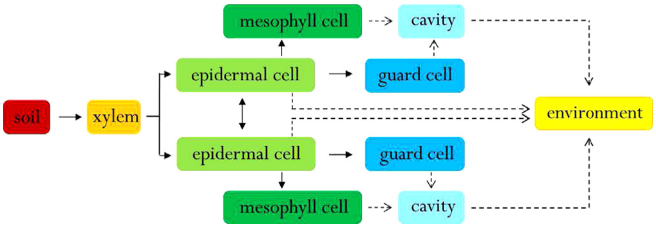

Fig. 1. Water flow pathway diagram. Solid and dashed arrows indicate water flows in the forms of liquid and vapor, respectively. The root between soil and xylem and leaf veins between xylem and epidermal cells are not specified. Water flows from xylem to mesophylls as well as between guard cells and mesophylls are not allowed.