

Comparing the dynamics of stomatal networks to the problem-solving dynamics of cellular computers

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Introduction

Is the adaptive response to environmental stimuli of a biological system lacking a central nervous system a result of a formal computation? If so, these biological systems must conform to a different set of computational rules than those associated with central processing. To explore this idea, we examined the dynamics of stomatal patchiness in leaves. Stomata—tiny pores on the surface of a leaf—are biological processing units that a plant uses to solve an optimization problem—maximize CO_2 assimilation for a given amount of H_2O loss. Under some conditions, groups of stomata coordinate in both space and time producing motile patches that can be visualized with chlorophyll fluorescence. These patches suggest that stomata are nonautonomous and that they form a network presumably engaged in the optimization task. In this study, we show that stomatal dynamics are statistically and qualitatively comparable to the emergent, collective, problem-solving dynamics of some cellular computing systems.

Stomatal Networks

Stomata are pores on the surfaces of leaves that permit the exchange of gases between the inside of the leaf and the atmosphere. In most plants, stomata are between 30 and 60 μm long and occur at densities between 50 and 200/ mm^2 . Figure 1 shows an image of a typical stomatal network. A stoma (singular) consists of two guard cells that change their shape, as a result of changes in internal water content via osmosis, thereby creating a pore of variable aperture. Gases diffuse through the open stomatal pores. For example, CO_2 enters the leaf, permitting photosynthesis to occur. At the same time, water vapor escapes. Excess water loss can have serious detrimental consequences for a plant, so plants are faced with a problem: under a given set of environmental conditions, how open or closed should the stomatal pores be?

Plants solve this problem on a daily basis by solving what has been formalized mathematically as a constrained optimization problem (Cowan and Farquhar 1977).

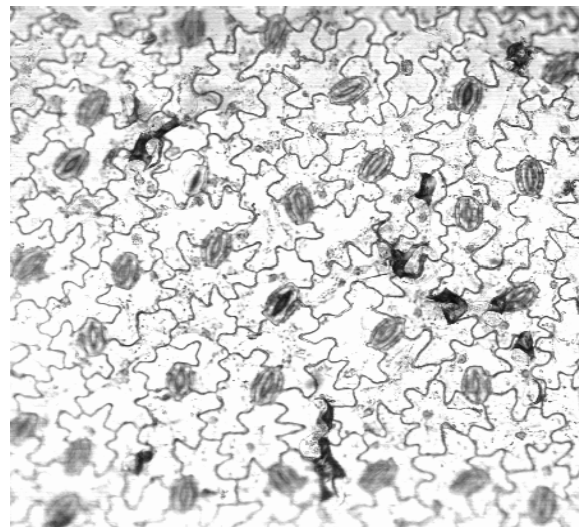


Figure 1. Stomatal network. The image (taken with a confocal microscope) shows stomata (the bean-shaped structures) separated by epidermal cells on the surface of a *Vicia faba* leaf. In this figure, the stomatal pore apertures are about 2 μm wide.

Traditionally, the constrained optimization model of plant biology treats stomata as autonomous units that respond independently to such environmental stimuli as light, CO_2 ,

humidity, and H₂O stress. In the traditional formulation, the model predicts that, as long as environmental changes are sufficiently slow, stomatal conductance, g (determined primarily by aperture), varies as environmental conditions change such that $\partial A/\partial g \propto \partial E/\partial g$ (where A is the rate of CO₂ uptake and E is the rate of water loss). It also predicts that the spatial distribution of g should be essentially uniform when environmental conditions are spatially uniform, varying only because of small structural differences in stomata. It has been shown, however, that groups of tens to thousands of stomata can behave drastically differently from stomata in adjacent areas even when environmental conditions are the same everywhere (Terashima 1992; Beyschlag and Eckstein 1998; Mott and Buckley 1998; Mott and Buckley 2000).

This spatially heterogeneous behavior is called “stomatal patchiness.” Stomatal patchiness can be dynamic, with complicated and apparently unpredictable spatial and temporal variations appearing over the leaf surface. Figure 2 shows an example of

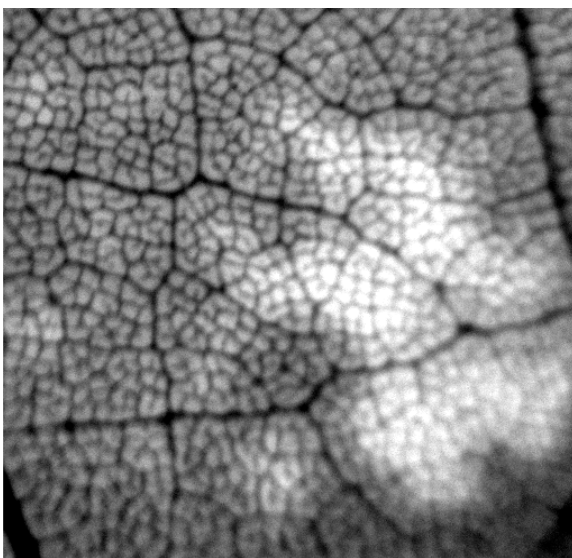


Figure 2. Patchy stomatal conductance.

In this chlorophyll fluorescence image of a Cocklebur (*Xanthium Strumarium*) leaf, open stomata appear as dark areas and closed stomata appear as light areas (the veins do not contain stomata). The area shown is 2.54 x 2.54 cm, and contains over 100,000 stomata.

stomatal patchiness with constant, spatially uniform environmental conditions. The figure, taken in the near infrared, is of chlorophyll fluorescence. Under carefully controlled conditions, chlorophyll fluorescence can be interpreted in terms of stomatal conductance (Daley, Raschke et al. 1989; Meyer and Genty 1998; West, Peak et al. 2004). Stomatal patchiness is inconsistent with the constrained optimization model. Nevertheless, it has been observed in over 200 species (Beyschlag and Eckstein 1998). Experiments have demonstrated that stomata can interact locally via hydraulic forces mediated by the epidermal cells between the stomata. Such forces may provide a mechanism for producing and sustaining the coordinated, stomatal behavior observed in patchiness (Haefner, Buckley et al. 1997; Mott, Denne et al. 1997; Mott, Shope et al. 1999).

Stomatal patches are often initiated by changing external humidity. In experiments that we have conducted where an abrupt, spatially uniform humidity decrease is applied to the leaf, we observe a variety of stomatal responses. In each case, the experimental region of the leaf starts in what appears to be a uniform steady state, with stomata approximately uniformly open. As a result of the applied humidity drop, stomata tend to close. How this closing is achieved, however, is remarkably variable. Often, all stomata tend to close more-or-less uniformly. In these cases, no patches are observed. Sometimes patches

form for a brief period, then quickly disappear. In rare instances, patches persist for hours and display rich dynamics. Which of the behaviors occurs in any one experiment is never predictable. The variability we observe suggests that stomatal dynamics is exquisitely sensitive to microscopic conditions that we cannot directly control—a situation that is reminiscent of space-time systems with self-organizing dynamics (Bak 1996). We presume that, in our experiments our plants start with a roughly uniform g_i , predicted by constrained optimization. After we lower the humidity, our plants presumably seek out a new, optimal g_f . We are interested in how the transition from g_i to g_f occurs, and the role (if any) patches play in it.

Cellular Computer Networks

An artificial cellular computing system consists of individual units, “cells,” usually arranged in a regular one- or two-dimensional lattice. Each cell is connected to some subset of other cells in the system. The states of the cells are updated simultaneously according to a deterministic rule. Depending on the degree of connectivity and the treatment of time, space, and state, a cellular computer can be categorized as a neural network (NN), a coupled map lattice (CML), a cellular neural network (CNN), or a cellular automaton (CA) (see Table 1).

Model Type	Space	Connectivity	Time	State
<i>Neural Network</i>	D	E	C	C
<i>Coupled Map Lattice</i>	D	E or L	D	C
<i>Cellular Neural Network</i>	D	L	C	C
<i>Cellular Automaton</i>	D	L	D	D

Table 1. Cellular Computer Networks. A categorization of different artificial cellular computer types based on their connectivity and treatment of space, time, and state. C=continuous; D=discrete; E=extensive; L=limited.

Cellular computing systems can perform global computational tasks. Depending on the degree of connectivity, the completion of that task can be non-trivial. For example, the performance of a global computation by an extensively connected network, where at any moment each cell has access to information from the entire system, is relatively simple. On the other hand, the same task performed by a strictly locally connected network, where at any moment each cell has access to a very limited amount of information from the entire system, is difficult. If the global behavior is not explicitly defined by the deterministic behavior of individual network units then the computation is said to be emergent (Crutchfield 1994). It has been shown that, in some locally connected CA that perform emergent computation, the global task is accomplished by “patches of information” coherently propagating over large distances (Crutchfield and Mitchell 1995). In these example systems (in which information is processed strictly locally), global computation is achieved because distant regions of the system can communicate via coherent patch propagation.

An instructive example of this is the density classification task performed by a two-state CA (Gacs, Kurdyumov et al. 1978; Crutchfield and Mitchell 1995; Sipper 1997). In one version of this task, the CA starts with any initial distribution of 0 and 1 states. The density of this initial configuration is said to be “classified” if the CA eventually evolves to a state of all 1s if the initial configuration had more 1s than 0s, and to all 0s, otherwise. Figure 3 shows an example of a two-dimensional CA performing density classification. In this

CA, each cell shares information with only a few of its nearest neighbors, yet the system as a whole manages to correctly assess that 1 was initially the majority state. No cell individually performs the density classification task in the CA shown: the global result emerges from the strictly local interaction of the component cells. Note that, shortly after the CA in Figure 3 begins to evolve, patches form and move coherently across the CA space.

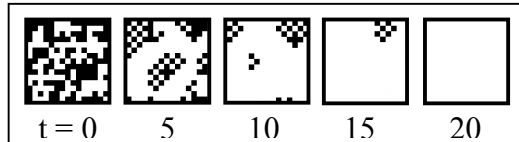


Figure 3. Density classification by a 2D CA. The configuration at $t = 0$ is a random distribution of 1s (white) and 0s (black) with $> 50\%$ 1s. As time progresses the CA evolves to a steady state of all 1s, indicating that 1s were initially in the majority.

In general, the farther the initial density is from 0.5 the more quickly and more accurately a density classifier CA will perform the classification task. For densities close to 0.5, the task becomes more difficult, though some CAs still perform fairly well even under these circumstances. We have made an exhaustive study of the behavior of very good 1D and 2D density classifier CAs for initial densities near 0.5. In our study, we start each time with exactly the same macroscopic initial density but with different microscopic configurations. In the vast majority of instances, these good classifiers quickly achieve a correct steady state. Much less frequently, the CAs take an inordinately long time (if ever) to reach steady state. The difference between two initial configurations that lead to rapid and protracted transients can be as little as two cells. Which initial configurations produce long transients is never predictable. In other words, density classifier CAs exhibit sensitive dependence on the microscopic details of their initial configurations.

A comparison of stomatal networks and cellular computer networks

Our discussion of stomatal networks and cellular computers identifies a number of suggestive similarities. Both are able to perform sophisticated global tasks even though distantly separated parts of the respective systems are not directly connected. Both show evidence of extreme sensitivity to microscopic system details. Both manifest dynamic patchiness, which, in the case of cellular computers, at least, is the mechanism by which global problem solving is accomplished. One wonders whether these similarities are merely accidental or if there are deeper, more quantitative connections between stomata and cellular computers.

To probe this question we have closely examined some of the statistical properties of the dynamics of these two different kinds of networks. Because stomata have continuous

aperture states that change asynchronously and continuously in time, while CAs have discrete states that change synchronously in discrete time, statistical similarities in their dynamics are not expected *a priori*. On the other hand, both stomata and CAs that compute appear to harbor the same kind of collective behavior that has been observed in simulations of self-organized critical systems (Bak, Tang et al. 1987). Taking a cue from such simulations, we have calculated Fourier spectra, Hurst's rescaled range (R/S) statistics, and event waiting distributions for both stomata and for several 1D and 2D density classifier CAs.

Data for stomatal networks were obtained from chlorophyll fluorescence images (512x512 pixels) from three different experiments during which extended dynamical patchiness occurred. We examined (512 entry) intensity time series for each of 50,000 randomly chosen pixels in our data sets. From these we calculated Fourier spectra and a summed power spectrum. The same data were used to calculate the Hurst R/S statistic. We defined an "event" as an unusually large change in pixel intensity (for a more detailed description see Peak, West et al. 2004) and calculated the distribution of time between successive events at each pixel.

The same statistics were calculated for 1D and 2D density classifier CAs. A good density classifier typically reaches steady state in a time that is too short to produce reasonable statistics. Thus, to protract the dynamics, we injected low amplitude white noise in the form of occasional random state flips. This perturbation introduces spurious high frequency variations in the dynamics, so care has to be taken to filter out its effects. Event waiting times were extracted from examples of unusually long, but unperturbed, transients. We defined an "event" in these studies as a change in patch type at a cell, specifically, as a time series of 1111 followed by a 0, or 0000 followed by a 1, or 1010 followed by a 0, or 0101 followed by a 1.

A summary of the statistical results is presented in Table 2. The spectral densities, $S(f)$, of the dynamics of all three network types (stomata, 1D and 2D CAs) have extended regions that are well fit by a power law, $S(f) \propto f^{-P_F}$, with exponents (P_F) ~ 2 . The Hurst exponent, H , of the power law expression $R/S \propto d^H$ (where d is the time delay) should be related to the spectral density exponent by $P_F = 2H + 1$. The calculated values of P_F and H for the 2D CAs we examined and for our stomatal networks fit this relationship well. The waiting time frequency distributions for the three network types are fit well by a power law, $F_W \propto W^{-P_W}$. In studies of self-organized dynamics it is found that the value of P_W depends sensitively on the specific details of the system (Christensen and Olami 1992). It is therefore not surprising that P_W for stomatal networks and density classifying CAs might be different. What is surprising is that these distributions are all power laws. The results presented here are strong evidence that stomatal networks and cellular computers are dynamically close cousins.

System	P_F	R^2	H	R^2	P_W	R^2
<i>Stomatal Network</i>	1.94 ± 0.10	0.99	0.60 ± 0.03	0.94	1.15 ± 0.21	0.93
<i>1-D CA</i>	1.98 ± 0.12	0.99	**	**	1.77 ± 0.23	0.91
<i>2-D CA Case 1</i>	1.99 ± 0.11	0.99	0.54 ± 0.02	0.99	2.22 ± 0.14	0.96
<i>2-D CA Case 2</i>	2.16 ± 0.12	0.99	0.60 ± 0.05	0.96	1.96 ± 0.11	0.97
<i>2-D CA Case 3</i>	1.91 ± 0.12	0.99	0.44 ± 0.05	0.96	2.73 ± 0.24	0.92
<i>2-D CA Case 4</i>	1.84 ± 0.17	0.99	0.35 ± 0.08	0.96	2.35 ± 0.19	0.93

Table 2. Statistical Summary. A summary of the statistical properties of stomatal networks and locally connected density classifying CAs that exhibit patches during the problem-solving process. P_F is the exponent of the power law expression $S(f) \propto f^{-P_F}$ fit to the Fourier spectra. H is the exponent of the power law expression $R/S \propto d^H$ where R/S is Hurst's rescaled range statistic and d is the time delay. P_W is the exponent of the expression $F_W \propto W^{-P_W}$ where F_W is the frequency of the waiting-time and W is the waiting-time. ** insufficient data to calculate this statistic.

Conclusion

Plants plausibly achieve an optimum stomatal aperture for a given set of environmental conditions. When a plant is presented with a “difficult problem” (e.g., an abrupt change in humidity), groups of stomata can form collective dynamical patches, contrary to the constrained optimization model of plant biology. We argue that the qualitative and quantitative features of stomatal patches are essentially indistinguishable from those found in locally connected cellular computers that perform global computational tasks. This leads us to conjecture that the reason so many plant species exhibit stomatal patchiness may be that, through their stomata, plants are performing a sophisticated kind of problem solving that is similar to emergent computation. Unambiguous resolution of this conjecture awaits the development of sharper tools than now exist for quantifying computation, especially as it exists in natural systems.

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