The Game of Leaf

Evidence that Stomatal Networks are Cellular Computers

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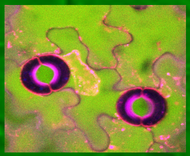
PLANT'S DILEMMA

- During photosynthesis a plant incorporates CO_2 from and loses H_2O to the atmosphere
- This dilemma can be framed as a **constrained optimization** problem
- Stomata are the hardware the plant uses to resolve this dilemma

STOMATA

- Tiny pores on the surface of a leaf
- Control H_2O and CO_2 exchange between leaf and atmosphere

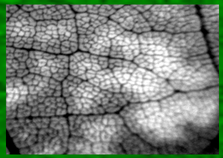


•Responsible for 99% of terrestrial carbon fixation and 90% of terrestrial water loss

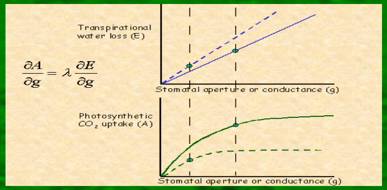
•Aperture size varies in response to light, CO_2, and humidity

STOMATAL NETWORKS

- Stomata interact through short range hydraulic and chemical signals—stomata form a **locally connected network**
- These connected networks show spatially coordinated behavior that change in time
- 512 by 512 grayscale image of chlorophyll fluorescence containing ~10^5 stomata—areas with open stomata are dark and areas with closed stomata are bright



CONSTRAINED OPTIMIZATION

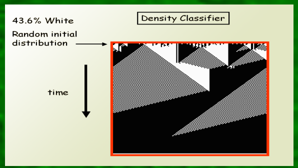


How does the plant do it?

CELLULAR COMPUTERS

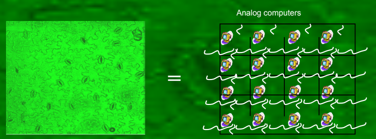
•Network of locally-connected processing information units that perform system wide computation—**emergent, distributed computation**

•Example: Density Classifier Automaton

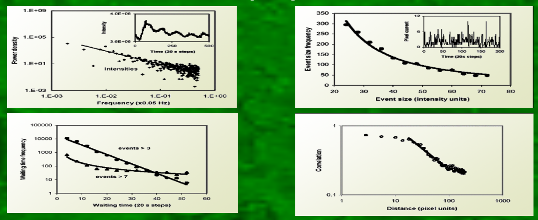


•Dynamics is **complex** and there are particles of information—**gliders**

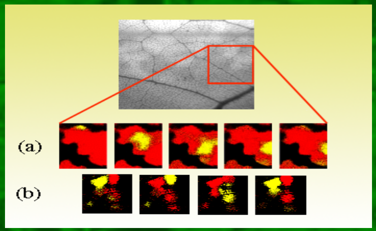
ARE STOMATAL NETWORKS CELLULAR COMPUTERS?



STOMATAL DYNAMICS IS COMPLEX (persistent correlations in time and space)



AND HAS GLIDERS



The Game of Leaf: Evidence that Stomatal Networks are Cellular Computers

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Some biological processes seem a lot like computation, but to date convincing evidence for this identification is lacking. To probe whether a network of *real* (as opposed to *simulated*) biological agents can plausibly be said to perform computation, we have experimentally studied the dynamics of the collective opening and closing of stomata on the surfaces of leaves of the plant *Xanthium strumarium L.* (cocklebur). Stomata are micron-size pores that regulate the exchange of gases between a plant's interior and the atmosphere. Stomata open in bright light, primarily to take in CO_2 for photosynthesis. A secondary consequence of stomatal opening is increased rate of water evaporation. Thus, a plant is continually confronted with a kind of cost-benefit problem: how should average stomatal aperture be adjusted (as environmental conditions vary) so that, in aggregate, sufficient CO_2 is taken up while excessive water loss is prevented. The plant's problem is exacerbated by its need to process and respond to heterogeneous information from widely separated parts without having a brain or central nervous system to oversee and coordinate such tasks.

We propose that plants may solve their global cost-benefit problem by "cellular computation." A cellular computer consists of spatially separated processing units (like stomata) that can share information among only a small number of local neighbors, yet, when properly "wired and programmed," can produce results relevant to the entire system. The dynamics of such "emergent, distributed computation" is characterized by persistent correlations in both space and time. Crucially, the dynamics also harbors coherently propagating data structures ("particles of information") that permit distant regions of the system to eventually communicate [1].

We used chlorophyll fluorescence as a spatially explicit probe of stomatal aperture. Chlorophyll fluorescence from leaves can be spatially patchy even under fixed, seemingly homogeneous, environmental conditions. The shape and intensity of fluorescence patches can vary over time and involve 10s to 1000s of stomata behaving in concert [2]. Stomata are clearly "wired together"—presumably through short-range hydraulic and chemical interactions—but are they programmed to compute? Our analyses of temporal and spatial correlations associated with patchy episodes reveal long-tail, power laws, as would be expected in cellular computation. In addition, by recoding our fluorescence images to detect intensity-change trends, we observe particle-like propagation of information over the surfaces of our leaves. We therefore conclude that collective stomatal dynamics is consistent with the view that leaves are computers.

[1] Boccara, N., Nasser, J. & Roger, M. (1991) *Phys. Rev.* **A44,** 866-875; Hanson, J. E. & Crutchfield, J. P. (1997) *Physica D* **103,** 169-189; Shalizi, C. R. & Crutchfield, J. P. (2001) *J. Stat. Phys.* **104,** 817.

[2] Cardon, Z. G., Mott, K. A. & Berry, J. A. (1994) *Plant Cell Environ.* **17,** 995-1008; Siebke, K. & Weis, E. (1995) *Planta* **196,** 155-165; Mott, K. A., Denne, F. & Powell, J. (1997) *Plant Cell Environ.* **20,** 1098-1107; Mott, K. A., Shope, J. C. & Buckley, T. N. (1999) *J. Exp. Bot.* **50,** 1207-1213