40 Satterlee, J.S. and Sussman, M.R. (1997) An *Arabidopsis* phosphatidylinositol 4-phosphate 5-kinase homolog with seven novel repeats rich in aromatic and glycine residues (Accession no. AF01938) (PGR 97–150). *Plant Physiol.* 115, 864
41 Franklin-Tong, V.E. *et al.* (1996) Growth of pollen tubes of *Papaver rhoeas* is regulated by a slow-moving calcium wave propagated by inositol 1,4,5-trisphosphate. *Plant Cell* 8, 1305–1321
42 Perera, I.Y. *et al.* (1999) Transient and sustained increases in inositol 1,4,5-trisphosphate precede the differential growth response in gravistimulated maize pulvini. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5838–5843
43 Rosen, E. *et al.* (1999) Root gravitropism: a complex response to a simple stimulus? *Trends Plant Sci.* 4, 407–412
44 Philippar, K. *et al.* (1999) Auxin-induced K^+ channel expression represents an essential step in coleoptile growth and gravitropism. *Proc. Natl. Acad. Sci. U. S. A.* 96, 12186–12191
45 Kaufman, P.B. *et al.* (1995) Hormones and the orientation of growth. In *Plant Hormones: Physiology, Biochemistry and Molecular Biology* (Davies, P.J., ed.), pp. 547–571, Kluwer
46 Patel, S. *et al.* (1999) Molecular properties of inositol 1,4,5-trisphosphate receptors. *Cell Calcium* 25, 247–264
47 Taylor, C.W. (1998) Inositol trisphosphate receptors: Ca^{2+}-modulated intracellular Ca^{2+} channels. *Biochim. Biophys. Acta* 1436, 19–33
48 Sanders, D. *et al.* (1999) Communicating with calcium. *Plant Cell* 11, 691–706
49 Dasgupta, S. *et al.* (1996) Interaction of myoinositoltrisphosphate-phytase complex with the receptor for intracellular Ca^{2+} mobilization in plants. *Biochemistry* 35, 4994–5001
50 Brearley, C.A. *et al.* (1997) Metabolic evidence for PtdIns(4,5)P_2-directed phospholipase C in permeabilized plant protoplasts. *Biochem J.* 324, 123–131
51 Drøbak, B.K. *et al.* (1991) Metabolism of inositol (1,4,5) trisphosphate by a soluble enzyme fraction from pea (*Pisum sativum*) roots. *Plant Physiol.* 95, 412–419
52 Gillaspy, G.E. *et al.* (1995) Plant inositol monophosphatase is a lithium-sensitive enzyme encoded by a multigene family. *Plant Cell* 7, 2175–2185
53 York, J.D. *et al.* (1999) A phospholipase C-dependent inositol polyphosphate kinase pathway required for efficient messenger RNA export. *Science* 285, 96–100
54 Loewus, F. and Murthy, P.P. (2000) myo-Inositol metabolism in plants. *Plant Sci.* 150, 1–19
55 Staxen, I. *et al.* (1999) Abscisic acid induces oscillations in guard-cell cytosolic free calcium that involve phosphoinositide-specific phospholipase C. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1779–1784
56 Chapman, K. (1998) Phospholipase activity during plant growth and development and in response to environmental stress. *Trends Plant Sci.* 3, 419–425
57 Berridge, M.J. *et al.* (1998) Calcium – a life and death signal. *Nature* 395, 645–648
58 Pliska-Matyshak, G. *et al.* (1997) Novel phosphoinositides in barley aleurone cells, additional evidence for the presence of phosphatidyl-*scyllo*-inositol. *Plant Physiol.* 113, 1385–1393
59 Tuominen, E.K. *et al.* (1999) Fluorescent phosphoinositide derivatives reveal specific binding of gelsolin and other actin regulatory proteins to mixed lipid bilayers. *Eur. J. Biochem.* 263, 85–92

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Patchy stomatal conductance: emergent collective behaviour of stomata

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Until recently, most scientists have tacitly assumed that individual stomata respond independently and similarly to stimuli, showing minor random variation in aperture and behaviour. This implies that stomatal behaviour should not depend on the scale of observation. However, it is now clear that these assumptions are often incorrect. Leaves frequently exhibit dramatic spatial and temporal heterogeneity in stomatal behaviour. This phenomenon, in which small 'patches' of stomata respond differently from those in adjacent regions of the leaf, is called 'patchy stomatal conductance'. It appears to represent a hitherto unknown type of emergent collective behaviour that manifests itself in populations of stomata in intact leaves.

Do stomata act independently regardless of the conduct of those around them? Or, do neighbouring stomata dictate their behaviour? Fifteen years ago, most stomatal physiologists would have assumed that stomata act independently, but recent discoveries now suggest that stomatal behaviour dictated by that of neighbouring stomata is also possible. Certainly, anyone studying stomatal responses at the level of the intact leaf would agree that stomata are complex and unpredictable, withstanding even the most determined efforts to understand their behaviour. Doubtless, this is partly because of the many environmental parameters that stomata respond to, and to the level of interaction among these responses. However, it now appears that some of this unpredictability might result from complex interactions between stomata, leading to a form of emergent behaviour that is inherently difficult to predict. This phenomenon, which we term 'patchy stomatal conductance', has been the subject of several recent exhaustive reviews[1–3]. This review will therefore focus on three aspects of the issue: hydraulic interactions as a mechanism for patchiness, the importance of scale in stomatal dynamics, and patchiness as an emergent collective property of stomata.

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Background

Stomata are formed by two specialized epidermal cells, termed guard cells, which are shaped like kidney beans in most dicots and like dumbbells in most monocots[4]. These cells dynamically regulate their concentration of osmotically active solutes to control turgor pressure and volume. As the turgor (and volume) of the guard cells increases, they bow apart to widen the pore. In general, stomatal responses are adapted to control the balance between carbon gain (CO_2 diffusion into the leaf) and water loss (H_2O diffusion out of the leaf), and they can also act to stave off dangerously low water potentials in leaves and runaway xylem cavitation by limiting transpiration[5,6]. To accomplish these tasks, stomata respond to several factors. First, guard cells respond directly to light intensity – increasing their solute concentration, and therefore stomatal aperture, as light intensity increases. They also respond to the concentration of CO_2 inside the leaf, but in this case the relationship is reversed: high concentrations of CO_2 cause solute efflux and therefore reductions in aperture size. These two responses interact when light intensity is increased.

Guard cells also respond to the rate of water loss from the leaf, closing at high transpiration rates and low humidities. Finally, guard cells close in response to the plant hormone, abscisic acid (ABA), which is synthesized in response to water stress and some other environmental stresses. The overall pore aperture under any given set of environmental conditions is a complex function of all these responses, and is made even more complex by circadian rhythms in stomatal sensitivity, delayed metabolism of ABA, and sensitivity to other plant hormones.

Appropriately, there has been substantial research into understanding the biochemical basis for changes in guard-cell solute concentration[7,8], and it is clear from these studies that individual guard-cell pairs do not require input from other guard cells to react to most environmental cues. Stomata do respond to some signals that originate in distant tissues; the most obvious example is ABA, which is synthesized in roots and mesophyll cells in response to water stress, and transported to guard cells in the transpiration stream. Other mesophyll signals have also been postulated (but none documented) to coordinate stomatal aperture with photosynthetic capacity[9]. Nevertheless, most stomatal responses seem to originate in guard cells, and require no input or interaction with surrounding epidermal tissue.

Given this focus on the individual guard cell as the functional unit for stomatal responses, the initial reports of 'patchy stomatal closure' were surprising. These studies indicated that water stress or applied ABA could cause stomata in discrete areas of the leaf to close substantially, whereas stomata in adjacent areas remained open[10,11]. Although variation in stomatal aperture over the leaf surface was known to exist before these studies, it was thought to be confined to broad gradients in aperture from one part of the leaf to another or simply small-scale random variation in apertures[2]. Furthermore, all stomata on the leaf appeared to respond similarly to environmental stimuli. Stomatal apertures on a leaf could apparently be treated as a coherent 'population' – a normal distribution whose mean shifted with environmental conditions, but whose variance was relatively constant[12,13]. Evidence that a contiguous group, or patch, of hundreds or thousands of stomata could defect from this population and respond differently and independently from neighbouring patches required a fundamental rethinking of how stomata function.

The first studies of patchy stomatal responses to water stress and ABA suggested a bimodal response: some areas of the leaf with nearly closed stomata and other areas with mostly open stomata. As such, it was easy to explain the effect by postulating differences in ABA sensitivity between stomata in different areas of the leaf. However, subsequent studies have shown that ABA-deficient mutants can exhibit this phenomenon[14]. Furthermore, patchiness can occur in response to many other stimuli, including low humidities and changes in light intensity[15,16].

The spatial and temporal complexity of patchy stomatal conductance is best revealed by sequential images of chlorophyll fluorescence, which mirror the spatial distribution of photosynthesis in a leaf [17,18] (Figs 1 and 2). Several common features emerge from such images. Patches are usually bound by leaf veins, and each patch has an apparently uniform conductance that is distinct from adjacent patches. Published studies have shown that the behaviour of conductance patches can be temporally stable, irregular and seemingly chaotic, or oscillatory. Patches can oscillate in or out of phase with other patches on the same leaf [19,20]. Interestingly, non-oscillating patches can be induced to oscillate in phase with distant patches on the leaf, implying some long-distance interaction[19]. Patches can also appear or disappear transiently or permanently, or arise *de novo* in unpredictable locations. In leaves with stomata on both surfaces, the pattern of patches can be different on both surfaces[21].

In short, the range of patch behaviours documented to date is extremely large. Coupled with the fact that patchiness can occur in response to several seemingly unrelated stimuli, this behavioural diversity makes it difficult to conceive a universal mechanism for the phenomenon.

A problem of scale

Patchy stomatal conductance escaped detection until recently because it occurs between the two scales at which stomata are most commonly and most easily studied. Because stomata are typically 20 to 50 μm long and occur at densities between 50 and 300 per mm^2 (Ref. 4), stomatal responses are usually studied either by observing individual stomata through a microscope, or by calculating stomatal conductance from whole-leaf gas-exchange data. However, microscopic studies of aperture can include only a few stomata at a time, and gas-exchange measurements typically average the responses of 10^5 stomata or more. Thus, neither of these methods provides spatially explicit information at the intermediate scale where patchy stomatal conductance hides. It is therefore not surprising that patchy stomatal closure was discovered by scientists trying to interpret measurements made at one scale in terms of processes at the other scale. A paradox emerged when leaf-level gas-exchange studies showed rapid and reversible changes in photosynthetic capacity after water stress or ABA treatments, while biochemical studies showed no effects. This inconsistency was resolved by questioning the familiar assumption that stomatal conductance is relatively uniform and normally distributed, and by recognizing that some patchy distributions of stomatal conductance can produce artifacts in gas-exchange calculations[10,11].

Patchiness makes measurements of stomatal behaviour highly scale-dependent. The summed effects of many patches with potentially different behaviours will determine the dynamics of whole-leaf stomatal conductance. For example, low-amplitude oscillations in whole-leaf stomatal conductance can reflect uniform behaviour (i.e. all stomata oscillating with low amplitude), or it can be caused by a few patches oscillating with large amplitudes or many patches oscillating slightly out of phase[19,20]. Whole-leaf stomatal conductance can even appear constant, in spite of large amplitude dynamics of some patches, if they are sufficiently out of phase with one another[19,22]. Patchy stomatal conductance can also affect whole-leaf carbon–water balance[23]. These effects are usually detrimental, but they can be essentially neutral or even slightly beneficial under some environmental conditions. Interestingly, patchiness is most often reported under these environmental conditions.

The difficulty in observing stomatal movements at the scale between individual stomata and gas exchange has prevented extensive study of stomatal patchiness, and even the most commonly employed techniques for studying the phenomenon have severe limitations. The earliest studies of patchy stomatal conductance used

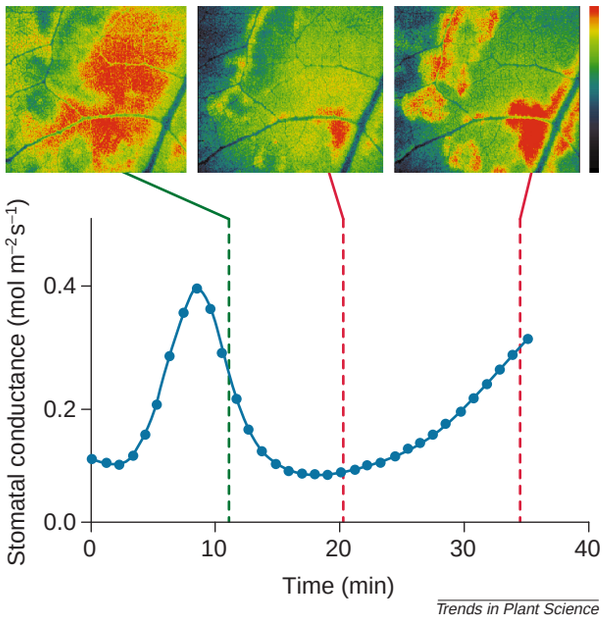

Fig. 1. Response of stomatal conductance to a step change in light intensity from darkness to 1000 μmol photons m^{-2} s^{-1} in *Xanthium strumarium*. Light was increased at time zero. The graph shows average stomatal conductance for the entire area of the leaf (6.25 cm^2) that was enclosed in the gas-exchange chamber. The images show the spatial distribution of photosynthesis for ~75% of the enclosed area. These images are derived from images of chlorophyll fluorescence (see Ref. 18 for more information), and the scale to the right of the images shows the relationship between pixel colour and photosynthetic rate as a percentage of the maximum. During all but the first 10 min of the experiment, the photosynthesis rate was related uniquely to the CO_2 concentration inside the leaf, and therefore to the stomatal conductance.

iodine staining to detect spatial variation in starch concentrations caused by sustained differences in photosynthesis between patches[10], or autoradiography to detect variation in photosynthetic $^{14}CO_2$ uptake[11]. However, these methods are destructive, and the former obscures short-term dynamics in patch patterns because starch metabolism is a relatively slow process. Another approach for detecting patchiness involves vacuum infiltrating leaves with water or other liquids[24]. This technique works on the principle that surface tension will prevent liquid from 'infiltrating' stomata that are nearly closed, but it yields only a binary result (infiltrated or not)[25], and like starch staining and autoradiography, is destructive and static. Furthermore, it has recently been shown that differences in the infiltration of areoles do not necessarily imply differences in their average conductance[25]. Most current work on patchy stomatal conductance uses yet another and more technically challenging method. Images of chlorophyll fluorescence provide a measure of the photosynthetic rate in different parts of the leaf and therefore yield indirect, spatially explicit measurements of stomatal conductance[17,18]. The advantage of this technique is that fluorescence can be observed nondestructively and thus dynamically (Figs 1 and 2). However, reliable inference of stomatal conductance from fluorescence intensity requires that there are no changes in mesophyll photosynthetic capacity, except those caused by changes in CO_2 concentration. Therefore, it is difficult to use this technique in experiments that affect photosynthetic capacity directly, such as changes in light intensity[26]. Finally, spatial variation in leaf temperature that results from differences in stomatal conductance has been used to detect patchiness[27], but like chlorophyll fluorescence imaging, this method is technically difficult, and its use is limited to conditions where stomatal conductance has large and consistent effects on leaf temperature.

Hydraulic interactions: a possible mechanism?

Often overlooked in studies of stomatal responses is the effect of epidermal-cell turgor pressure on pore aperture. In contrast to the effect of guard cells, increases in epidermal turgor decrease pore aperture because they exert backpressure, which the guard cells must overcome in order to open the pore. For equal changes in the turgor pressure of both guard and epidermal cells, the epidermal cells have the upper hand; that is, if turgor is increased equally in both epidermal and guard cells, the pore will close slightly[28,29]. This leads to some interesting dynamics in stomatal behaviour. For example, when a leaf is subjected to a sudden decrease in ambient humidity, the transpiration rate increases and rapidly draws water from both the guard and epidermal cells. Turgor pressure drops quickly and roughly equally in both cells, and the pore opens initially. In the longer term (over the course of many minutes), guard cells reduce their turgor through a reduction in osmotic pressure, and this overcomes the initial opening to cause an overall reduction in pore aperture – consistent with the stomatal mandate to conserve water. In some cases, interactions between these two feedback loops can cause damped or sustained oscillations in stomatal apertures[30,31].

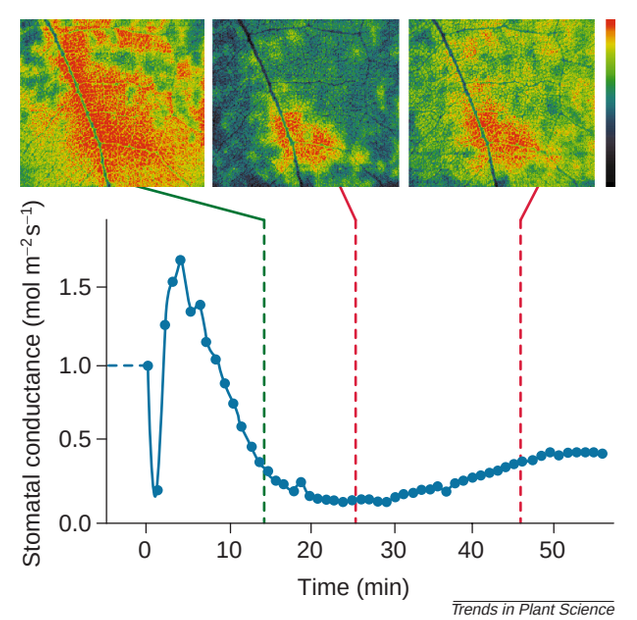

Fig. 2. Response of stomatal conductance to a step change in humidity from 37 mmol mol^{-1} to 18 mmol mol^{-1} in *Xanthium strumarium*. Humidity was changed at time zero. At all times during the experiment, photosynthesis rate was uniquely related to the CO_2 concentration inside the leaf, and therefore to the stomatal conductance. The graph shows average stomatal conductance for the entire area of the leaf (6.25 cm^2) that was enclosed in the gas-exchange chamber. The images show the spatial distribution of photosynthesis for ~75% of the enclosed area. These images are derived from images of chlorophyll fluorescence (see Ref. 18 for more information), and the scale to the right of the images shows the relationship between pixel colour and photosynthetic rate as a percentage of the maximum. During all but the first 10 min of the experiment, the photosynthesis rate was related uniquely to the CO_2 concentration inside the leaf, and therefore to the stomatal conductance.

It has been suggested that the initial positive-feedback phase of this loop might serve to coordinate stomatal movements[22]. If changes in the aperture of one pore can substantially affect the turgor pressure of epidermal cells that push inwards on adjacent stomata, then an increase in the aperture of one stoma (or several stomata) might trigger a slight increase in the aperture of adjacent stomata (Fig. 3). The feedback loop would metastasize to encompass an ever-larger area of epidermis until a vein is encountered. The vein would present an impassable ridge of high water potential. Thus, the behaviour of stomata within an areole (the smallest area of a leaf completely surrounded by veins) would tend to be coordinated.

This hypothesis has been tested by perturbing a single stoma with a small stream of dry air and observing the effects on nearby stomata that experience no such perturbation[32]. These experiments showed that stomata that experienced constant environmental conditions responded to perturbations of adjacent stomata and that the responses were consistent with the hydraulic mechanism described above. More-recent data show that the turgor pressure of epidermal cells around the unperturbed stomata responds in a manner consistent with the hypothesis (K.A. Mott and P.J. Franks, unpublished). Other evidence for hydraulic coupling between stomata has come from studying the response of stomata in a single areole to a change from darkness to high light intensity levels[33]. After the light is increased it takes a while (up to ~60 min) before guard-cell turgor overcomes the epidermal backpressure, creating a lag before the pore opens. This lag period is shorter and less variable under conditions of low air humidity, which should intensify hydraulic coupling. These results suggest that stomata with short lag times reduce epidermal turgor within the areole, thus hydraulically coercing their neighbours to open sooner.

Hydraulic interactions might serve to coordinate stomata within an areole or patch, but how does the behaviour of different patches on a leaf become uncoordinated? It is possible that random spatial variation in stomatal characteristics could translate into random differences between areoles in the average or dominant mode of stomatal behaviour. In support of this idea, a computer model of stomatal functioning that incorporated local hydraulic interactions and random variation in stomatal characteristics produced spatial patterns in stomatal conductance that resembled patchy stomatal conductance[22]. However, in the model, the temporal behaviour of areoles varied only slightly, and a considerable amount of time was required for the conductance of individual patches to diverge enough to produce a patchy pattern. Thus, other factors must be contributing to the dynamics of patches on a larger scale.

It has been hypothesized that hydraulic interactions between areoles on a leaf might provide the missing piece to this puzzle[34,35]. A change in conductance (and thus transpiration rate) in one areole will draw down the water potential in surrounding veins. This might strongly influence nearby areoles, but will generally have a smaller effect on distant areoles. However, because of the reticulate venation in most dicot leaves, many areoles will receive water from several directions, and it seems possible that changes in transpiration for a particular areole might have complex effects on other areoles, independent of proximity. Suppose that the environment of the leaf is perturbed, and a handful of randomly scattered areoles happen to respond more dramatically than others (because of randomly different average mechanical properties of the stomata in those regions). Changes in the partitioning of water between areoles, through the network of veins, could produce the erratic behaviour of patches often seen in leaves. Thus, vascular flow dynamics might provide the link between the small scale (individual stomata and areoles) and the large scale (the whole leaf), and could therefore play an important role in creating the emergent spatial dynamics of patchy stomatal conductance.

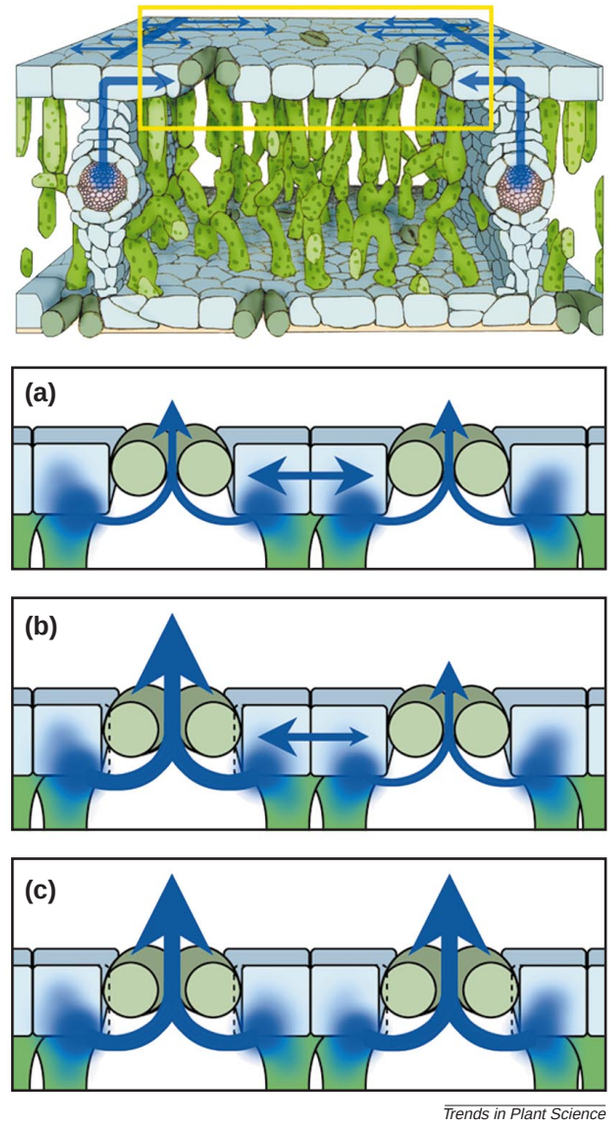

Fig. 3. Hydraulic coupling among stomata. Yellow inset-area depicted in (a–c). In (a), both stomata are slightly open. In (b), the stoma on the left has increased its aperture (and transpiration rate) in response to some perturbation, and the turgor of the adjacent epidermal cells has decreased. (c) An increase in transpiration from the stoma on the left reduces the epidermal turgor for the stoma on the right, allowing it to open slightly. The resulting increase in transpiration from both stomata would cause a further reduction of epidermal turgor, thereby propagating the effect until a vein is reached. Stomatal opening will be eventually limited by feedback loops. Blue arrows denote water flow.

Complexity and predictability

Leaves, and on a larger scale, canopies, should operate like an ideal gas: an enormous assembly of independent units, varying randomly but uniform in basic properties; individually complex and unpredictable but collectively simple and predictable. Yet, to the dismay of scientists who wish to predict biotic responses at these more-complex levels, plants do not meet these requirements – they are not even close.

Patchy stomatal conductance shows that the behaviour of things as seemingly elementary as a single leaf can be rather nonlinear and heterogeneous, and can defy dynamic prediction based on the

linear 'ideal gas' paradigm. Complex systems theory is a useful perspective for studying patchiness, because complexity is concerned with 'emergent collective properties' – properties that result from interactions between small-scale units and cannot be predicted by the analysis of their isolated behaviours[36]. These emergent properties can make observed relationships between variables dependent on the scale of measurement[37,38]. And they often involve dynamic coordination in time (e.g. oscillations) or space (e.g. patchiness), which implies the existence of metascale dynamics (dynamics that are manifest between familiar scales of interest or observation, but which are caused by the interaction of small- and large-scale dynamics).

Any system of interacting parts lives on a continuum between two extremes. At one extreme, the components are totally independent. Here the system dynamics are independent of scale, and can be understood and predicted by linear mathematics[36]. Any structure at intermediate scales is coincidental. At the other extreme, the components interact so strongly that every change in one component is felt by all the others. In this case, the dynamics are also predictable on a large scale, but it is because the system is coordinated rather than random and disjunct. Therefore a system that is too weakly connected will generate only uninteresting, scale-independent randomness, whereas one that is too tightly constrained by global rules will generally yield predictable and uniform dynamics.

The middle ground is where interesting, unpredictable, emergent properties are born, and here is where we see patchy stomatal conductance. The reticulate network of veins that supplies water to dicot leaf tissues might represent an intermediately connected system somewhere in the middle of this continuum. Could patchy conductance be caused, at least in part, by scale-dependent flow properties through this network? The answer to this question awaits further research.

References

1 Terashima, I. (1992) Anatomy of non-uniform leaf photosynthesis. *Photosynth. Res.* 31, 195–212

2 Weyers, J.D.B. and Lawson, T. (1997) Heterogeneity in stomatal characteristics. *Adv. Bot. Res.* 26, 317–351

3 Beyschlag, W. and Eckstein, J. (1998) Stomatal patchiness. In *Progress in Botany* (Behnke, K. *et al.*, eds), pp. 283–298, Springer-Verlag

4 Meidner, H. and Mansfield, T.A. (1968) *The Physiology of Stomata*, McGraw-Hill

5 Jones, H.G. and Sutherland, R.A. (1991) Stomatal control of xylem embolism. *Plant Cell Environ.* 14, 607–612

6 Sperry, J.S. (1995) Limitations of water transport and their consequences. In *Plant Stems: Physiology and Functional Morphology* (Gartner, B., ed.), pp. 105–120, Academic Press

7 Leckie, C.P. *et al.* (1998) Second messengers in guard cells. *J. Exp. Bot.* 49, 339–349

8 McAinsh, M.R. and Hetherington, A.M. (1998) Encoding specificity in Ca^{2+} signalling systems. *Trends Plant Sci.* 3, 32–36

9 Wong, S-C. *et al.* (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* 282, 424–426

10 Terashima, I. *et al.* (1988) Characterisation of non-uniform photosynthesis induced by abscisic acid in leaves having different mesophyll anatomies. *Plant Cell Physiol.* 29, 385–394

11 Downton, W.J.S. *et al.* (1988) Non-uniform stomatal closure induced by water stress causes putative non-stomatal inhibition of photosynthesis. *New Phytol.* 110, 503–509

12 Laisk, A. *et al.* (1980) Statistical distribution of stomatal apertures of *Vicia faba* and *Hordium vulgare* and the Spannungsphase of stomatal opening. *J. Exp. Bot.* 31, 49–58

13 Gorton, H.L. *et al.* (1988) Repeated measurements of aperture for individual stomates. *Plant Physiol.* 89, 387–390

14 Eckstein, J. *et al.* (1998) Abscisic acid is not necessarily required for the induction of patchy stomatal closure. *J. Exp. Biol.* 49, 611–616

15 Eckstein, J. *et al.* (1996) Changes in photon flux can induce stomatal patchiness. *Plant Cell Environ.* 19, 1066–1074

16 Bro, E. *et al.* (1996) Heterogeneity of leaf CO_2 assimilation during photosynthetic induction. *Plant Cell Environ.* 19, 1349–1358

17 Daley, P.F. *et al.* (1989) Topography of photosynthetic activity of leaves obtained from video images of chlorophyll fluorescence. *Plant Physiol.* 90, 1233–1238

18 Genty, B. and Meyer, S. (1994) Quantitative mapping of leaf photosynthesis using chlorophyll fluorescence imaging. *Aust. J. Plant Physiol.* 22, 277–284

19 Cardon, Z.G. *et al.* (1994) Dynamics of patchy stomatal movements, and their contribution to steady-state and oscillating stomatal conductance calculated with gas-exchange techniques. *Plant Cell Environ.* 17, 995–1008

20 Siebke, K. and Weis, E. (1995) 'Assimilation images' of leaves of *Glechoma hederacea*; analysis of non-synchronous stomata related oscillations. *Planta* 196, 155–165

21 Mott, K.A. *et al.* (1993) Asymmetric patchy stomatal closure for the two surfaces of *Xanthium strumarium* L. leaves at low humidity. *Plant Cell Environ.* 16, 25–34

22 Haefner, J.W. *et al.* (1997) A spatially explicit model of patchy stomatal responses to humidity. *Plant Cell Environ.* 20, 1087–1097

23 Buckley, T.N. *et al.* (1999) Carbon-water balance and patchy stomatal conductance. *Oecologia* 118, 132–143

24 Beyschlag, W. and Pfanz, H. (1992) A fast method to detect the occurrence of nonhomogenous distribution of stomatal aperture in heterobaric plant leaves. Experiments with *Arbutus unedo* L. during the diurnal course. *Oecologia* 82, 52–55

25 Lawson, T. *et al.* (1998) The nature of heterogeneity in the stomatal behavior of *Phaseolus vulgaris* L. primary leaves. *J. Exp. Bot.* 49, 1387–1395

26 Meyer, S. and Genty, B. (1999) Heterogeneous inhibition of photosynthesis over the leaf surface of *Rosa rubiginosa* L. during water stress and abscisic acid treatment: induction of a metabolic component by limitation of CO_2 diffusion. *Planta* 210, 126–131

27 Jones, H.G. (1999) Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant Cell Environ.* 22, 1043–1055

28 Sharpe, P.J.H. *et al.* (1987) Stomatal mechanics. In *Stomatal Function* (Zeiger, E. *et al.*, eds), pp. 91–114, Stanford University Press

29 Franks, P.J. *et al.* (1998) A study of stomatal mechanics using the cell pressure probe. *Plant Cell Environ.* 21, 94–100

30 Cowan, I.R. (1972) Oscillations in stomatal conductance and plant functioning associated with stomatal conductance: observations and a model. *Planta* 106, 185–219

31 Delwiche, M.J. and Cooke, J.R. (1977) An analytical model of the hydraulic aspects of stomatal dynamics. *J.Theor. Biol.* 69, 113–141

32 Mott, K.A. *et al.* (1997) Interactions among stomata in response to perturbations in humidity. *Plant Cell Environ.* 20, 1098–1107

33 Mott, K.A. *et al.* (1999) Effects of humidity on light-induced stomatal opening: evidence for hydraulic coupling among stomata. *J. Exp. Bot.* 50, 1207–1213

34 Mott, K.A. and Buckley, T.N. (1998) Stomatal heterogeneity. *J. Exp. Bot.* 49, 407–417

35 Buckley, T.N. and Mott, K.A. (2000) Stomatal responses to non-local changes in PFD: evidence for long-distance hydraulic interactions. *Plant Cell Environ.* 23, 301–309

36 Kaufmann, S. (1995) *At Home in the Universe*, Oxford University Press

37 Farquhar, G.D. (1989) Models of integrated photosynthesis of cells and leaves. *Philos. Trans. R. Soc. London Ser. B* 323, 357–367

38 McNaughton, K.G. and Jarvis, P.G. (1991) Effects of spatial scale on stomatal control of transpiration. *Agric. Forest Meteorol.* 54, 279–301

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