POWER AND SYRED/SPL

Plants regulate important processes such as photosynthesis through pores called stomata.

PLANT SCIENCE

# Rediscovering the bush telegraph

**Ian T. Baldwin** assesses three books on the rich array of plant behaviours, from sensing to communication.

**Leaf Defence**
EDWARD E. FARMER
*Oxford Univ. Press: 2014.*

**Plant Sensing and Communication**
RICHARD KARBAN
*Univ. Chicago Press: 2015.*

**Plant Behaviour and Intelligence**
ANTHONY TREWAVAS
*Oxford Univ. Press: 2014.*

The food writer Michael Pollan, author of *The Omnivore's Dilemma* (Penguin, 2006) among others, wrote an article in *The New Yorker* in 2013 exploring why terms such as intelligence, memory and even behaviour have been contentious for plant scientists. His thesis boils down to a divide in biology that allows zoologists to use anthropomorphic terms, but denies the privilege to plant scientists. Pollan allies himself with a small band of intrepid researchers crusading against the "cerebrocentric" view that permits behaviour only to organisms with brains. He tells of collateral damage from sensationalist treatments that exaggerate plant-science findings, and of glimmers of a new sensitivity towards all life.

Pollan identifies an interesting story about the development of an emerging scientific field, and the baggage that scientists bring to their work. The idea that plants are 'smarter' than their immobility suggests is now supported by rigorous experimentation and fieldwork that are uncovering the genes and chemicals that mediate plants' environmental intelligence. We know now that much of a plant's rich behavioural repertoire is hard to observe because it is played out in a chemical arena. Plants overcome the constraints of immobility mainly by harnessing their prowess as synthetic organic chemists. For instance, floral scents contain compounds that attract pollinating animals and repel flower-eating ones. Nectar is a brew of nutrients and toxins that optimize the behaviour of pollinators. Much of the relevant literature is now synthesized in three books by leading researchers in the field: Edward Farmer's *Leaf Defence*, Anthony Trewavas's *Plant Behaviour and Intelligence* and Richard Karban's *Plant Sensing and Communication*.

## RESEARCH RENAISSANCE

The research is essentially a rediscovery. Between the eighteenth and the twentieth centuries, Erasmus Darwin, Charles Darwin and botanists Wilhelm Pfeffer and Jagadish Chandra Bose published books that brim with observations on plant behaviour. Charles Darwin's 1880 *The Power of Movement in Plants*, for instance, incorporates insights from his experiments on how exposure to light drives bending in grasses, which laid the foundation for the discovery of the hormones responsible for plant movement. If they were alive today, these scientists would wonder what all the fuss is about.

The study of plant defences was revived in 1959, when entomologist Gottfried Fraenkel published the landmark article 'The raison d'être of secondary plant substances' (G. S. Fraenkel *Science* **129,** 1466–1470; 1959), building on original insights by nineteenth-century botanist C. Ernst Stahl.

Fraenkel argued that plants' awesome diversity of secondary metabolites such as toxic alkaloids and aromatic terpenoids evolved primarily to thwart herbivores. He ushered in the modern era of chemical

ecology, including an exuberance of theory to explain these metabolites' patterns of accumulation. Much of the theorizing came from zoologists, who applied paradigms from animal-behaviour studies to plants, often without deeper understanding of how plants function as organisms. The plant-biology community had little patience for this, being at the time focused on understanding mechanisms of plant growth under controlled laboratory conditions, developing *Arabidopsis* as a model plant and embracing molecular biology. After reading Farmer, Karban and Trewavas's books, I felt that the prevailing scientific opinion that plants are mere autotrophic growth machines has perhaps as much to do with the divorce between molecular and organismic approaches as with the botany–zoology divide.

*Leaf Defence* considers why plants have or lack leaves, and why leaves evolved to have particular traits. Because leaves dominate most plants' above-ground biomass, herbivores usually home in on them, a circumstance that has shaped leaves' chemistry, physics, morphology and development. Plants, meanwhile, eat sunlight with their leaves. So to fathom leaf evolution, it is important to understand both herbivores' digestive tracts and the dynamics of solar radiation.

Farmer works on jasmonates, a fatty-acid-based signalling system that activates many of plants' defences against herbivores. *Leaf Defence* provides an excellent review of the rapidly evolving literature in this field. The only disappointment is that books do not evolve as rapidly even as the literature from the author's own lab. Farmer's book was written before his laboratory reported a landmark discovery: a molecular link between jasmonate signalling and electrical signalling induced by herbivore attack (S. A. R. Mousavi *et al. Nature* **500,** 422–426; 2013).

Farmer weaves his compelling narrative from hard-core molecular research on mechanisms of perception of herbivore attack and defence responses, to more speculative inferences about how leaf colour and escape to rocky outcrops help plants to survive the relentless interests of herbivores. He highlights the lack of evidence for some sensationalist stories of plant–plant signalling, such as one about signalling between South African acacia trees about impending attacks from antelopes. And of the three books, *Leaf Defence* is the only one to include structures of plant chemicals.

The plant 'behaviour' debate described by Pollan is the starting point for the other two books. In *Plant Sensing and Communication*, Karban, a behavioural ecologist and entomologist, discusses environmental elements to which plants are thought to respond, such as light and sound. Karban, who featured prominently in Pollan's article, largely avoids political melodrama, instead providing clear working definitions of some of the contentious vocabulary: communication, eavesdropping, learning and memory. His summaries of plants' sensory abilities — such as the cues and signals that they use to adjust to the environment — retain an evolutionary perspective. And he branches out into areas such as mate choice, for example detailing how plants selectively breed with specific fathers represented in a mixed pollen load.

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To hear more about Anthony Trewavas, visit:
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Karban's research interests overlap with mine; we even work on the same species (coyote tobacco, *Nicotiana attenuata*). Although he is a gifted writer and synthesizer, Karban's review of the research on the mechanisms of plant perception and response is not well served by his lack of familiarity with the techniques that uncover them. Issues that he identifies as central unsolved problems (such as whether the volatile 'alarm calls' of plants protect against herbivores and increase fitness under real-world conditions) have been solved and published. The unrealistic experimental designs so common in the early literature are frequently reported uncritically. In discussing the complicated process of demonstrating an adaptation, Karban does not mention the genes responsible for the expression of traits such as shade avoidance, or the advantages offered in this area by cheap sequencing. So I recommend *Plant Sensing and Communication* to those who want a low-calorie introduction and a deeper consideration of the concepts, but the primary literature is better for understanding the mechanisms.

## BOTANICAL MECHANICS

Trewavas, by contrast, moves effortlessly from mechanistic research to invigorating insights into real-world plant behaviour. *Plant Behaviour and Intelligence* is a wild ride, covering ground from the origins of life to intelligent nutrient-foraging behaviour in the roots of higher plants. Trewavas's five decades of research into plants' molecular biology and physiology, and their evolution as self-organizing systems, make him fully 'phytomorphized'. He thinks like a plant, effortlessly calling on specific traits to look at how plants solve problems in similar ways to social insects — from siphonogamy (in which pollen tubes carry sperm cells to egg cells) to highly dispersed sensory systems. He celebrates behaviour in plants while avoiding "animal envy". At 76, Trewavas may have written his last book — but it is one that encapsulates his life's work beautifully.

*Plant Behaviour and Intelligence* is also peppered with references to classics in the field, and takes inspiration from the geneticist Barbara McClintock's "feeling for the organism", which she derived from her long study of maize (corn) and discovery of 'jumping genes', or transposons. Trewavas and Farmer share a deep understanding of how plants function, mechanistically and biochemically, and this anchors their forays into how plants work in the real world. This grounding in mechanism may prove to be the key to convincing a scientific community sensitized to the gap between populist hype and the data on plant behaviour.

**Charles Darwin systematically investigated plant behaviour in the late nineteenth century.**

Plant biology is emerging from its *Arabidopsis*-in-the-laboratory phase. Researchers need to understand the natural-history context of such models before plant behaviours can be sensibly scrutinized in the functional (natural) context. The infusion of ideas from behavioural ecology between 1950 and 1990 revived the field, but it now needs balance. The mental constructs that ecologists bring to experimentation on plant function, such as the cost–benefit paradigm applied to resource allocation, are of limited value when they are unmoored from the mechanisms that anchor these phenotypes. These three books suggest that the way forward may be through a return to the observational skills that allowed the great researchers of the twentieth century to become phytomorphized. ■

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