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PLANT SCIENCE

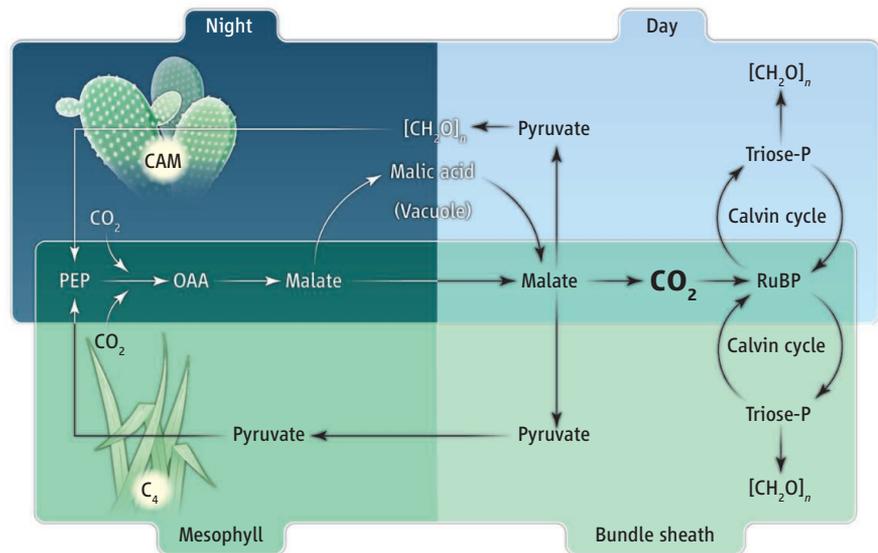
Photosynthesis, Reorganized

Mary Jane West-Eberhard,¹ J. Andrew C. Smith,² Klaus Winter³

Photosynthesis—the conversion of carbon dioxide (CO₂) into organic compounds using energy from sunlight—occurs via three pathways in terrestrial plants. The most common and ancient of these is C₃ photosynthesis, whereas C₄ photosynthesis and crassulacean acid metabolism (CAM) are derived from C₃. Despite great taxonomic diversity across plants that use C₄ and CAM photosynthesis, the core biochemical characteristics of each are similar in many independent plant lineages. How does such convergent biochemistry arise? Shared biochemical properties suggest that C₄ and CAM photosynthesis may have arisen through the reorganization of metabolic processes already present in C₃ plants. Modified expression of these processes would have been subject to selection and genetic accommodation in producing the distinctive derived phenotypes.

CAM plants conserve water by conducting most of their gas exchange in the relatively cool atmosphere at night, allowing, for example, succulent agaves and cacti to grow in strongly water-limited semidesert habitats and supporting many species of epiphytic bromeliads and orchids in microclimatically arid niches in tropical forests (1). C₄ plants benefit from the elimination of photorespiration and grow more rapidly than their C₃ relatives in hot environments in the tropics and subtropics (2). Economically important CAM plants like pineapple, agaves (sisal, tequila), and orchids (vanilla), and C₄ plants like maize, sugarcane, and sorghum, can thus grow under conditions less suitable for C₃ plants such as rice, wheat, and barley. And some may have potential as bioenergy crops (3).

In C₃ photosynthesis, atmospheric CO₂ is captured by ribulose-1,5-bisphosphate carboxylase–oxygenase (RuBisCO), the first enzyme in the Calvin cycle, through which inorganic carbon is fixed into organic form within the chloroplasts of leaf mesophyll tissue. C₄ and CAM photosynthesis involve auxiliary mechanisms outside the chloroplasts that fix atmospheric CO₂ via a phosphoenol-



Similar separations. The CO₂-concentrating mechanisms (for delivery to the Calvin cycle) in CAM (top) and C₄ (bottom) plants are temporally and spatially separated, respectively. [CH₂O]_n, carbohydrates; OAA, oxaloacetate.

pyruvate carboxylase (PEPC)—malate pathway before delivering it at increased concentration to RuBisCO in the chloroplast. This maximizes the carboxylation activity of RuBisCO while suppressing the wasteful photorespiratory oxygenase activity of this bifunctional enzyme.

The CO₂-concentrating mechanisms of C₄ and CAM plants depend on the same feature—separation of the auxiliary CO₂-fixation process from the Calvin cycle (see the figure). In C₄ photosynthesis, the separation is spatial. Fixation of CO₂ by PEPC occurs in mesophyll cells; the four-carbon products such as malate or aspartate diffuse to the adjacent thick-walled bundle-sheath cells where RuBisCO is localized, and where CO₂ is released by decarboxylation. In CAM plants, the separation is temporal. PEPC is active at night, producing malic acid that is sequestered in large intracellular vacuoles; the following day the plant's gas-exchange pores (stomata) close, malic acid is released from the vacuole, and CO₂ is available at enhanced concentrations for fixation by RuBisCO.

Among the angiosperms (flowering plants), C₄ photosynthesis has evolved more than 45 times in 19 families (4), and CAM in more than 30 families (1), with multiple origins even within plant families such as

Comparative physiology suggests that reorganization and co-option of ancestral traits drove diversification of C₄ and CAM photosynthesis.

the bromeliads (5) and orchids (6). As in many other organisms, the repeated independent origins of C₄ and CAM photosynthesis may have been possible due to evolution by reorganization (7, 8)—the co-option and modification of ancient metabolic pathways. Such modifications can be initiated by mutation or by environmental change, and then accommodated, under selection, by genomic change as the adaptive phenotype evolves (8). Although C₄ and CAM photosynthesis are considered major evolutionary innovations, few, if any, of their essential components are completely new (4, 9, 10). All of the enzymes required in these pathways appear to be homologs of ancestral forms found in C₃ species (9–11). Gene duplication, alternative splicing of mRNA, and changes in cis-regulatory elements or enhancers that control gene expression can maintain essential ancestral functions alongside new ones (7).

Genes from C₃ species may already possess the cis-regulatory elements necessary for recruitment into C₄ photosynthesis (“conserved functional latency”) (12), requiring only modification of a trans-acting factor to produce cell-specific expression. The distinctive temporal patterns of gene expression in CAM plants might be gov-

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erned by transcription factors implicated in the endogenous circadian rhythm of these plants (13).

However, reorganized expression of ancestral pathways only partly explains the recurrent origins of C_4 and CAM. Particular morphological and biochemical variants may have facilitated the increased compartmentalization of the Calvin cycle that allows auxiliary carbon concentration to work, and may help explain why C_4 and CAM are phylogenetically separated rather than interspersed within the lineages where they recur. Does such reorganization begin with a new mutation, or can environmental stress induce the expression of a new pathway using preexisting genetic variants? The close C_3 relatives of C_4 and CAM plants are key species for answering such questions. In some plants, CAM photosynthesis is envi-

ronmentally inducible and facultative (14), and several examples exist of C_3 - C_4 “intermediates,” typically from marginal arid or saline habitats (4). Therefore, perhaps a primordial version of CAM or C_4 could originate as a response to environmental stress in a subpopulation of C_3 individuals genetically disposed to express it, exploiting the standing or cryptic genetic variation (15) already present in the population. This would help to explain the examples of convergent evolution at the molecular level in multiple independent lineages of C_4 grasses (11). Reflections on the evolutionary origins of C_4 and CAM photosynthesis may also help refine genetic research and expand its possibilities.

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CELL BIOLOGY

Cytonemes Show Their Colors

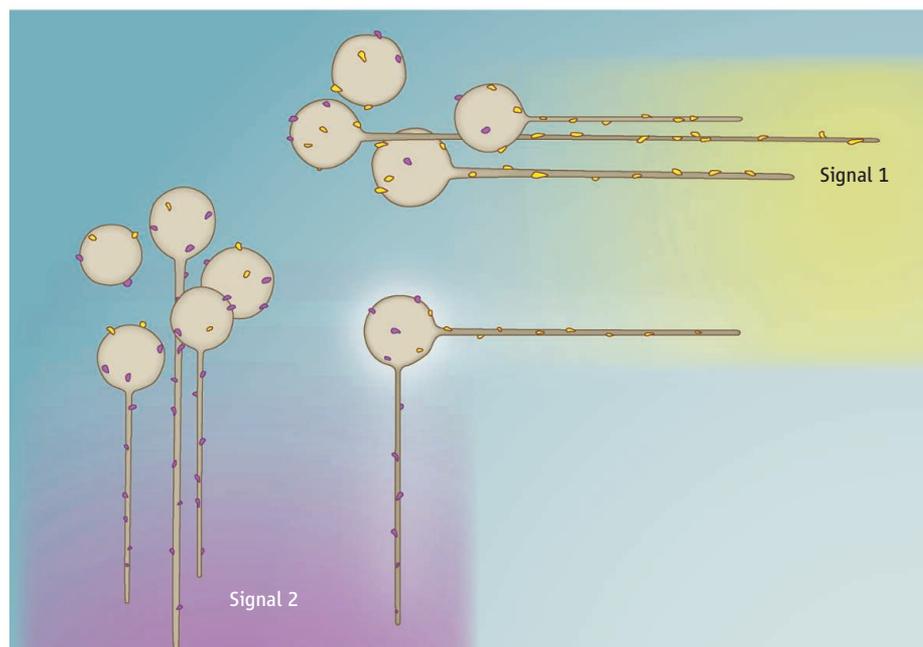
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Cells in multicellular organisms need to communicate in order to generate organs and tissues of appropriate shape and function. The “information” content of the communication consists of modulating the activity of biochemical signaling pathways. The “hardware” that is used to convey and collect such signals sometimes includes specialized structures, such as the synapses of neurons and molecular complexes that enable cells to adhere to each other or other surfaces. In many instances, cells actively explore their environment by producing extensions such as filopodia, lamellipodia, axons, and dendrites. The exact role of such extensions in non-neuronal cells remains, in most cases, unexplored. On page 354 of this issue, Roy *et al.* (1) help fill in some of the blanks. They report on the properties of filopodial extensions in the wing, eye, and tracheal system of *Drosophila*. They show that these extensions are dedicated to certain signaling pathways by the segregation of the corresponding receptors on their surfaces. The authors call these cell projections, which are based on the protein actin, cytonemes (Latin for “cell thread”). Their

findings point to a scenario in which cells produce a signaling molecule that triggers other cells in the vicinity to form cytonemes, which ultimately become stable and are used for propagating specific intercellular signals.

In developing *Drosophila*, cells create extensions dedicated to specific signaling pathways.

The exclusive, nonoverlapping localization of specific signaling receptors to dedicated cytonemes comes as a surprise, especially because cells often express receptor components for many pathways, potentially



Reaching out. Cells exposed to a gradient of a chemical signal (purple shading, lower left, and yellow shading, upper right) extend thread-like structures called cytonemes with surface receptors (purple and yellow ovals) toward the signal source. Cytonemes specialize to propagate a specific signal. Researchers speculate that some cells could extend multiple types of cytonemes, each carrying a different signal.

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