Photosynthesis

Casting new light on old relationships

Peter D. Moore

THE ecological significance of the biochemical routes by which photosynthetic plants fix atmospheric carbon has been the subject of considerable debate. It now seems that the simple classification of plants into one of three photosynthetic types, C3, C4 and CAM, is less distinct than has been thought. Recent experiments by Ueno *et al.*[1] and by Groenhof *et al.*[2] suggest that closely related taxa may differ in their photosynthetic pathways, and that in some plants C4- and CAM-type systems can be induced by appropriate environmental stresses.

Under conditions of high light, high temperature and drought, plants that use the enzyme phosphoenolpyruvate carboxylase (PEPC) for the initial fixation of carbon — C4 and CAM plants — are at a distinct advantage over C3 species. PEPC allows CAM plants to fix carbon in the dark, enabling them to keep their stomata closed during the day. In C4 plants, there is a spatial rather than a temporal separation of the initial and final fixation process via the Calvin cycle, which takes place only in specialized vascular bundle sheath cells, an arrangement termed Kranz anatomy. Both types of photosynthesis have the advantage of the high affinity of the PEPC enzyme for carbon dioxide, and thus have low carbon dioxide compensation points. They also avoid the problems of photorespiration experienced by C3 plants. The ability to scavenge for carbon results in a further potential ecological advantage of PEPC-based systems — they can compete efficiently in aquatic habitats where carbon is often in short supply.

It has long been recognized that closely related taxa may differ in their photosynthetic systems. In 1972 Hatch *et al.*[3] described hybridization experiments between *Atriplex patula* ssp. *hastata* (a C3 species) and *Atriplex rosea* (a C4 species). They studied isoenzyme patterns of hybrids and concluded that "at least some of the enzymes necessary for the operation of the C4 pathway are unique isoenzyme entities evolved specifically for that purpose".

Frean and Marks[4] have examined taxa that are even more closely related, indeed that are considered mere variants of a single grass species, *Alloteropsis semialata*, and yet which exhibit C3 and C4 photosynthesis and have normal and Kranz anatomy, respectively. Chromosome squashes of pollen grains from these two variants, however, show that the C3 form is a fertile diploid ($2n = 18$) and the C4 form is an allohexaploid ($2n = 54$). So the taxonomic difference is greater than one might have supposed and involves polyploidy. Perhaps they should even be regarded as separate species.

Groenhof, Bryant and Etherington[5] have brought attention to a succulent CAM species, *Sedum telephium*, which can move from a photosynthetic mixed economy with both day and night carbon fixation to a full nocturnal CAM mode when subjected to water stress. They now show[2] that this switch is accompanied by a substantial increase in dark-period PEPC activity. They also show that two species of the PEPC protein are involved, one (the CAM species) a monomer and the other a dimer.

Progress is also being made on the aquatic front. Ueno *et al.*[1] have described a species of spike rush (*Eleocharis vivipara*) from Florida which can grow in both terrestrial and submerged conditions. They find that the terrestrial form has specialized sheath cells and conducts C4 photosynthesis. But the submerged form appears to fix carbon using the Rubisco enzyme and has anatomy more characteristic of a C3 species. They carried out reciprocal experiments in which they put submerged forms in terrestrial conditions and vice versa, and the plants reverse both their anatomical and biochemical forms.

These results contrast with the findings of Keeley and Busch[6] using the pteridophyte *Isoetes*, where the submerged form uses a CAM system of photosynthesis. Because the great advantage of carbon fixation by PEPC in aquatic conditions is the ability to compete for carbon when it is in short supply, often in the middle of the day, it would be interesting to know whether *Eleocharis vivipara* retains a C3 system in submerged conditions when starved of carbon. The results do suggest, however, that not only is the biochemical pathway of C4 inducible, but so is the Kranz anatomy. □

1. Ueno, O., Samejima, M., Muto, S. & Miyachi, S. *Proc. natn. Acad. Sci, U.S.A.* **85**, 6733–6737 (1988).
2. Groenhof, A.C., Bryant, J.A. & Etherington, J.R. *Ann. Bot.* **62**, 187–192 (1988).
3. Hatch, M.D., Osmond, C.B., Troughton, J.H. & Bjorkman, O. *Yb. Carnegie Instn. Wash.* **71**, 135–141 (1972).
4. Frean, M.L. & Marks, E. *Bot. J. Linn. Soc.* **97**, 255–259 (1988).
5. Groenhof, A.C., Bryant, J.A. & Etherington, J.R. *Ann. Bot.* **57**, 689–695 (1986).
6. Keeley, J.E. & Busch, G. *Plant Physiol.* **76**, 525–530 (1984).

Peter D. Moore is Reader in Ecology in the Division of Biosphere Sciences, King's College, Campden Hill Road, London W8 7AH, UK.

Daedalus

Strains of sweet music

WHY do we like music? Alone among aesthetic experiences it means nothing, and has no obvious grounding in our instinctive nature. And yet it is probably the most moving and magical of all the arts.

Daedalus reckons that our musical sense evolved when we still lived in trees. The simplest way of telling if a tree is rotten, say, or a branch strong enough to swing on, is to sense its vibrations. A stable structure, well inside its elastic limit, will vibrate linearly, with harmonics in integral ratios and no intermodulation. A branch on the point of breaking, however, will be grossly nonlinear. Its discordant harmonics, and its intermodulation of superimposed frequencies, must bring immediate instinctive alarm to a tree-creature venturing onto it. The fundamental vibrations of a tree can only be sensed with hands or feet, but our ancestors must soon have learnt to listen for higher modes, or to tap or strike the wood to excite them. A tuneful harmonic outcome spelt safety; a discordant one deadly peril. And so the love of harmony entered the human soul. Some people can still appreciate music purely by its vibrations against the skin, and we all instinctively judge the soundness of an object by giving it an exploratory bash.

So, says Daedalus, creatures who live in trees should be musical. Song-birds are obviously on his side; and DREADCO's zoologists are presenting a course of musical appreciation to an audience of koala bears, three-toed sloths, squirrels, tree-frogs, and so on, to look for interest in these species as well. But his theory has clear technological implications too. It suggests a simple, non-destructive means of stress-testing any structure *in situ*. Just vibrate it at a specific frequency, and listen to the harmonics.

A trained ear should be good enough. The old violin makers used to tap a tree to judge if its wood was fit for their purpose. Those hi-fi fans who are really offended by 0.01 per cent of intermodulation distortion should easily be able to sense how far into its nonlinear region a piece of wood has been stressed. But electronic frequency measurement is more accurate still. DREADCO's technicians are testing a simple device that injects two tones into a structure at any point, and measures their intermodulation product: a measure of the local curvature of the stress–strain curve. This shows where the material is on that curve, and hence — what the engineer really wants to know — how much more stress it can take. Scanned over bridges, vehicles and all sorts of similar structures in service, the DREADCO anharmonograph will detect the highly stressed bits before they break.

David Jones