

SWITCHBACK EVOLUTION AND PHOTOSYNTHESIS IN ANGIOSPERMS

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Abstract: Switchback evolution, phylogenetically repeated activation and repression of a prepatter, seems the most likely explanation of the scattered occurrence of C_4 photosynthesis among unrelated angiosperms.

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There are two main pathways of carbon fixation in angiosperms. One is found in all angiosperms and other plants. Here the Calvin cycle results in the production of phosphoglycerate, which has a backbone of three carbon atoms. In many monocots and a few dicots, however, compounds with four carbon atoms are first produced by a process which involves many biochemical rearrangements and a characteristic tissue anatomy of the photosynthetic structures (Black, 1973; Brown, 1975). These processes are called C_3 and C_4 respectively. A few C_3 species have the usual tissue anatomy of C_4 species and at least one C_4 species has a tissue anatomy rather like that of C_3 species (Shomer-Ilan, Beer, and Waisel, 1975). There are about three fairly distinct biochemical variants of C_4 metabolism (Hatch, Kagawa and Craig, 1975; Hatch, 1976), although many structural and biochemical features are common to all C_4 plants (Hatch, 1978). The species frequently of C_4 grasses has a surprisingly close correlation with minimum July temperature (Teeri and Stowe, 1976), while C_4 dicots are more closely associated with aridity (Stowe and Teeri, 1978). Many of the C_4 species belong to the Gramineae, but there is great taxonomic and phylogenetic scatter of this derived phenotype both within and especially outside this family (Downton, 1975).

There are five possible explanations for this phylogenetic scatter. One is that the phylogeny is wrong and should be changed so that all C_4 species form one clade. This alternative would do such violence to other kinds of evidence that it can be dismissed. So can the alternative that the C_4 condition is primitive and has been lost in all but the tips of a number of phyletic twigs. A third possibility, the one commonly accepted (e.g. Smith and Robbins, 1975; Grimwade, 1977), is that the entire C_4 biochemical and structural complex arose many (perhaps 20) times independently. So much convergence would be involved in each case that a simpler evolutionary topology should be found if possible. The convergence isn't a matter of merely having the same adaptive result, but of getting it in one of a very few complex and similar ways every time. Nevertheless, if the new regulation of enzymes in one C_4 clade differs from the corresponding regulation in other C_4 clades more than it does from its presumptively ancestral regulation in related C_3 species, this alternative must be accepted for such species.

The two other alternatives each involve a single origin for the C_4 character complex. In one, the regulatory genes for the complex are physically close together and are occasionally transferred from one group of plants to another, probably by viral transduction. In the other, the regulatory genes have been present in most or all lineages of angiosperms,

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including all those leading to present C_4 clades, but their phenotypic expression is suppressed in C_3 species. Probably in some C_3 species (perhaps most dicots) C_4 genes would change too much for an easy reversal even when advantageous, while in others the transition back would be easier. Expression or repression of the genetic prepatter could perhaps in some cases be controlled by even a single switch gene. The enzymes of the C_4 pathway occur also in C_3 species, but the recurrent pattern of their regulation and that of the characteristic morphology must itself be genically controlled. It is this latter control which the fifth hypothesis addresses.

The number of regulatory genes controlling the development of the C_4 complex is unknown but probably more than the very few involved in known cases of transduction. If the genes occur on different chromosomes (cf. Björkman, 1976), transduction is unlikely for this reason also.

I favor the fifth hypothesis. It invokes no improbable coincidences and depends on known mechanisms. The switching on and off of gene complexes is a commonplace in developmental genetics. An obvious example involves sexual differentiation in dioecious species, in a few of which a single gene does act as a switch. Retention of an unexpressed prepatter for millions of years is less well known, but I have reviewed some apparent examples of it (Van Valen, 1970; see also Shapiro, 1978). Unless the regulatory genes of the C_4 complex are also involved in other processes, under different control, one would expect them to accumulate deleterious mutations and perhaps deletions, gradually making it more difficult to reactivate the C_4 complex. Perhaps this is why C_4 species vary in their decarboxylation mechanisms (on which see Hatch, 1976); similarities at this level may perhaps more often be convergent. The occasional occurrence of species with an incomplete C_4 complex (Kennedy and Laetsch, 1974; Brown, 1976) is also to be expected, as with the third hypothesis, even if such species aren't derived from hybrids.

The wide phylogenetic scatter of C_4 species suggests that the complex arose very early in angiosperm history, probably in the early Cretaceous. The reported advantage of C_4 metabolism under conditions of high light and temperature, and low water (Moore, 1978), interestingly parallels the best-supported hypothesis for the ancestral habitat of angiosperms: open, semi-arid, and warm, perhaps tropical (Doyle, 1977). A third photosynthetic pathway, crassulacean acid metabolism (CAM), occurs mostly in desert succulents. It has appreciable biochemical similarities to C_4 metabolism (Laetsch, 1974) and the two modes never occur in the same species (Beevers, 1976), although they can occur in different species of one genus (Webster, Brown and Smith, 1975). All C_4 and CAM plants also use the C_3 pathway. CAM plants lack the characteristic C_4 morphology. In some species CAM is facultative, being induced by an appropriate photoperiod or osmotic stress (Osmond, Winter, Lüttge, Winter, and Troughton, 1978). At other times it is inactive in such species, just as I hypothesize for at least the common information of CAM and C_4 metabolism in C_3 species. CAM is phyletically scattered, perhaps not as much as is C_4 metabolism although it occurs in as many families. A report of its occurrence in a fern (see Black and Williams, 1976) is based only on CO_2 fixation in darkness, unsupported by biochemical information.

The best groups for a direct test of the hypothesis of repressed prepatterns would be C_3 species closely related to C_4 (or CAM) ones. In both the C_3 and C_4 species of such sets, genetic information of both complexes should be present in an undamaged state. Hybridization or other

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means may sometimes be feasible for activation of the presumptively repressed complexes. Polytypic species would be optimal but none are yet known. Björkman (1976) has reported some results of crosses between a C₃ and a C₄ species of Atriplex. They rule out a single switch gene here but the crosses couldn't be carried far enough to give hope of any information on whether the controllers of expression in the C₄ species had any effect on the C₃ species.

In at least one species young leaves are C₃ and old leaves are C₄ in all respects, intermediate leaves being intermediate (Raghavendra, Rajendrudu, and Das, 1978). This shows the existence of a unified regulatory switch here, as do the seasonal and other inducible changes in some CAM species.

I suggest that evolution involving phylogenetically repeated activation and repression of a prepattern be called switchback evolution. Switchbacks are zigzag segments of railroads which climb very steep hills, with Y-shaped switches at the end of each zig or zag instead of turns. At each switch the train reverses direction.

Switchback evolution may be uncommon but is probably less rare than it seems. In most cases it would be difficult to distinguish on one side from convergence, or on another side from continuous expression. The degree of developmental novelty can give suggestive evidence to distinguish switchback evolution from convergence, but critical evidence must come from actual phylogenies, appropriate genetic crosses, or activation of the presumptively repressed prepattern. When switchback evolution is confused with continuous expression the optimally estimated phylogeny may be wrong. Switchback evolution is perhaps more likely than convergence to produce false reconstructions of phylogenies, because the characters are homologous and perhaps identical in different taxa as well as having little reconstruction on complexity.

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