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Heritable Repression due to Paramutation in Maize

In the penetrating analysis and interpretation of paramutation at the R locus in maize by Brink, Styles, and Axtell (1), information that I have presented on the phenomenon at the B locus is briefly considered. Although the B data clearly show that paramutation in this system and others might well be interpreted as a meiotic and terminal phenomenon, the interpretation of Brink, Styles, and Axtell is that all paramutation is somatic (or, rather, premeiotic), and that the data for B do not raise doubt on this point. Related comments are needed also on their conclusion that paramutation at the R locus cannot involve transfer of particles between alleles. Only when these mechanical features of paramutation are defined will it become clear whether paramutation systems involve typical or unique mechanisms of gene regulation, and whether the biological significance of paramutation is ontogenetic or phylogenetic.

Paramutation at the B locus occurs late in ontogeny. This conclusion rests on clear evidence, partly phenotypic and partly developmental (2). Examples cited by Brink, Styles, and Axtell from several plant species in support of an opposite conclusion all depend on the conventional view that somatic sectoring demonstrates the occurrence of paramutation in the mitosis at which the sector was delimited. As discussed elsewhere (2), differential mitoses that result in sectors may be differential in the potential for paramutation, rather than in the paramutation event itself. Similar delayed timing in repression-control systems has been found by McClintock (3) in the "presetting" phenomenon, in which a gene is programed at one stage of development to function subsequently in patterned concert, even as late as in the next generation. The B data show that all or most of a life cycle can intervene between the formation of the paramutational heterozygote and the paramutation event. Consequently, the question of whether paramutation can be generalized as premeiotic (or as meioticterminal) is entirely open. Definitive experiments identifying the exact stages of the events have not yet been devised.

The mechanics of paramutation at the R locus are discussed by Brink, Styles, and Axtell (1). Their data show that increase in functional capacity of R, which, they hypothesize, reflects loss of repressor elements, occurs in Rr heterozygotes. Since the same change occurs in deficiency heterozygotes (R-), loss of repressors, they point out, cannot be occurring by transfer to the absent homologous region. Brink, Styles, and Axtell argue that transfer is thereby excluded as a mechanical process for all R paramutation. However, the changes that can be interpreted as due to gain of repressors occur only in the presence of R^{st} or alleles with more repressors. Whether paramutation is meiotic or premeiotic, through contact or otherwise, a mechanical process by which gain occurs must be considered, and gain of elements by transfer is a conceptually economical hypothesis for the mechanics of change of R to R'. According to this view, loss of elements could be permitted by the Rr or Rcondition, since no supply of elements would be provided by the allele. The data do not warrant disposal of the transfer model.

The late timing of paramutation at the B locus and the interpretation of particle transfer have led to the suggestion (2) that release of a repressor element (from B') is triggered at or near meiosis, and that the element then transfers to the allele (B). The mechanical process in terminal pigmenting cells can be viewed as parallel to that in germinal cells but as less efficient, perhaps due to the absence of synapsis. A model of the kind suggested below, even though unduly exact, may express this repressor-transfer view less abstractly. Stent (4) has suggested that appended messenger RNA may act as a repressor, and more recently Bonner and Widholm (5) have presented evidence for chromosomal RNA that is organ-specific and complementary to nuclear DNA; this chromosomal RNA may be an integral part of gene repression systems. In parallel with repression by end-product feedback in bacteria (6), repressor (RNA or otherwise) released from a heritably repressed gene (B', R', R^{st}) could transfer as feedback to the allele (B, R) and append to the DNA. Since the genetic software (the repressing material) must be able to replicate along with the gene it represses, one would suppose that appended RNA might be capable of replication in place. Transfer of such a repressor, either by contact or by release and migration, would be entirely reasonable and not incompatible with either the R or the B information.

Exact materials and mechanics for paramutation can be hypothesized, and there will be differences of opinion about the hypotheses. There is full agreement, however, on this important fact: potential for genetic activity can be altered by the history of a gene, and associated software appears to be responsible in both of the cases that have been thoroughly studied.

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References and Notes

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Oceanic Basalt Leads and the Age of the Earth

In a recent report Ulrych (1) claims to have derived an "independent age for the earth." He states that the significance of his calculations is that the "age" which he obtains for the earth is independent of the age of the samples used in the calculations. It is true that his method does not require an independent determination of the length of time that a related series of rocks have spent in the crust, as long as their original source was homogeneous from T_0 (the time at which the gross structure of the earth developed) until the time at which the rocks were derived from the source, T_1 (the age of the samples). However, the absence of an independent criterion for determining that this condition is met introduces several problems.