

Genetic Estimate of Cellular Autarky

Viable, morphological mutants may be used for studies of gene controlled differentiation. Such mutants have been abundant in all higher organisms wherever they have been sought. There is virtually no information, however, on the molecular control of development in higher organisms. Mutations of 'dispensable genes' have been extremely useful in elucidating biochemical pathways in fungi and bacteria. Several attempts have been made in microorganisms to estimate the frequency of dispensable genes, which can be compensated by simple chemical substances fed to the cell. In *E. coli* 23% (LEUPOLD and HOROWITZ¹) and in *Neurospora* 46% (HOROWITZ and LEUPOLD²) of the temperature sensitive functions were reparable on complete nutrient media. ATWOOD and MUKAI³ tested the observations made on the special class of temperature sensitive mutants for validity in a large spectrum of mutations in *Neurospora*. They employed the heterokaryon method whereby recessive lethal nuclei were balanced by the wild type alleles and the resulting homokaryotic conidia were tested for repair on a complete medium. Only 7 out of 190 (3.7%) UV-induced mutants and 2 out of 26 (7.7%) spontaneous mutants were compensated for growth requirements on the complete medium. MARROW⁴ re-examined the problem and suggested that the unnatural heterokaryotic condition may have debilitated several semilethal genes. Therefore the differences in frequency obtained by the temperature sensitivity and heterokaryon methods may be partly explained.

These lower organisms are not well suited for morphogenetic studies. It is important to know how many of the common, non-lethal genes, affecting differentiation in higher plants could be normalized by exogenous supply of nutrients. *Arabidopsis thaliana* is a useful organism for such investigations since large numbers of morphological mutants are available. In addition the plant can be cultured to maturity under aseptic conditions on chemically well defined media (RÉDEI⁵).

Eight viable mutants were subjected to a test comparable to some extent to that of ATWOOD. Seeds heterozygous for recessive chromosome markers were irradiated with 13,000 r X-rays after 24 h inhibition on wet filter paper. Somatic sectors resulting from deletion or mutation of the wild allele or mitotic recombination etc. (HIRONO and RÉDEI⁶) were scored (Table).

No sectors would be expected if the original mutation prevented the synthesis of diffusible substances. Heterozygotes for all the tested markers displayed sectors, however. The frequency of the different type of sectors can not be identical since mutation rates vary according to loci, deletions may be produced by one or two hit events depending on the location of the gene in the chromosome, chances of recombination depend on gene centromere distances etc. Physiological factors also influence the detectability of sectors: some color spots are easier to observe than leaf shape modifying sectors.

By the cross-feeding from one sector to another all essential nutrients which would pass through cell membranes should reach the mutant tissues if produced in excess. If any diffusion from cell to cell takes place sharp boundaries between sectors is not expected. If phenotypic repair can not be accomplished in the chimera there is little chance to change the mutant phenotype by providing nutrients in a 'complete medium'. The man made complete medium is not expected to match the composition of the solutes of a normal cytoplasm; in addition the normal tissue should provide the nutrients selectively timed.

All the 8 tested genotypes produced clearly demarcated sectors. Because of the small number of mutants tested it is not known exactly how many of the whole spectrum of the viable mutants are involved in cell limited genetic defects. There is, however, 0.995 probability that less than half of a similar random sample of mutants are reparable in function and 0.900 is the probability that maximally 25% of the viable mutants could be successfully cross-fed from somatic sectors. It is pertinent to note that from the approximately 2000 viable and lethal mutants of *Arabidopsis* tested on a complete medium in our laboratory only about 2% responded to exogenous supply of nutrients. These figures are in reasonable agreement with the estimates of ATWOOD³ in *Neurospora* but appear to be lower than those of WALLIS⁷ who succeeded to repair 6 out of 37 (16%) barley mutants on amino acid containing media. Still it seems that the great majority of mutants are irreparable even with the most perfect feeding techniques. Since the frequency of modifiable or reparable genetic functions is so low, a study of the mechanism of morphogenesis and differentiation of specific structures appears difficult by culture methods providing normal metabolites^{8,9}.

Frequency of somatic sectoring in irradiated heterozygotes of *Arabidopsis*

Linkage group	Marker	Population	No. of sectorial plants
2	er (compact growth, blunt fruits)	1808	1
2	as (asymmetric leaves)	1808	10
2	su (yellow)	1808	67
3	ca (yellow green)	1400	14
3	vi (round leaf, dark green)	1400	1
3	gl ¹ (glabrous)	1400	6
4	ch ¹ (chlorophyll b deficient)	845	12
4	pa (dwarf, dark green)	845	2

Résumé. Huit mutants récessifs viables de l'*Arabidopsis*, une plante supérieure, traités par rayons X en hétérozygotie ont produit des secteurs somatiques distincts. Il semble aussi que la majorité des mutations viables sont des produits de gènes limités aux cellules.

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¹ U. LEUPOLD and N. H. HOROWITZ, Z. VererbLehre 84, 306 (1952).

² N. H. HOROWITZ and U. LEUPOLD, Cold Spring Harb. Symp. quant. Biol. 16, 65 (1951).

³ K. C. ATWOOD and F. MUKAI, Proc. natn. Acad. Sci. USA 39, 1027 (1953).

⁴ J. MARROW, Science 144, 307 (1964).

⁵ G. P. RÉDEI, Am. J. Bot. 52, 834 (1965).

⁶ Y. HIRONO and G. P. RÉDEI, Genetics 51, 519 (1965).

⁷ B. WALLIS, Hereditas 50, 317 (1963).

⁸ Contribution from the Missouri Agricultural Experiment Station, Journal Series No. 5048. Approved by the Director.

⁹ Supported by the United States Atomic Energy Commission Contract AEC AT (11-1)-1609.