

procedure, despite frequent and exhaustive discussions with each group of workers. One notable point of interest, however, is the relatively large differences in the ADP : O ratios, particularly with wheat, obtained by the different groups. The ADP : O ratios quoted in this paper (2.2) are lower than those obtained by Sarkissian and Srivastava (3.0-6.0)³ and Sage and Hobson (3.0). We suspect that further investigation of this discrepancy will eventually help to resolve the controversy concerning mitochondrial complementation.

The conclusion from our investigations is that we have been unable to demonstrate mitochondrial complementation, despite paying careful attention to published procedures. Until the phenomenon is better understood and the experimental conditions necessary for its expression more accurately described, we cannot, at present, recommend that mitochondrial complementation be used in a hybrid cereal breeding programme.

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- ¹ McDaniel, R. G., and Sarkissian, I. V., *Science*, **152**, 1640 (1966).
- ² McDaniel, R. G., and Sarkissian, I. V., *Genetics*, **59**, 465 (1968).
- ³ Sarkissian, I. V., and Srivastava, H. K., *Proc. US Nat. Acad. Sci.*, **63**, 302 (1969).
- ⁴ McDaniel, R. G., in *Barley Genetics II* (edit. by Nilan, R. A.), 323 (Washington State University Press, 1970).
- ⁵ Hobson, G. E., *Biochem. J.*, **124**, 10 P (1971)
- ⁶ McDaniel, R. G., *Nature New Biology*, **236**, 190 (1972).
- ⁷ Sarkissian, I. V., and Srivastava, H. K., *Genetics*, **57**, 843 (1967).
- ⁸ Sarkissian, I. V., and Srivastava, H. K., *Life Sci.*, **8** (II), 1201 (1969).

An Increasing Fitness Function for a Population with Many Niches

THE mean viability, V , increases from generation to generation¹⁻³ for a single autosomal locus with multiple alleles. Ewens⁴ has recently proved that for an arbitrary number of linked loci, with viability additive over loci, mean viability is again increasing. This latter result was proved using the former.

Here I show a further case in which a fairly simple fitness function increases from generation to generation. Levene⁵ formulated a model in which there were a number, m , of niches. Mating was at random amongst the total population, the resultant offspring migrating to the niches, which were of relative size c_i , and being subject to selection in those niches.

In a population in which there are n alleles A_j ($j = 1, 2, \dots, n$), and the viability of the $A_j A_k$ genotype in the i th niche is a_{ijk} , p_j is the frequency of the j th allele just before mating, and p_j' is the frequency one generation later, then⁶

$$p_j' = \frac{\sum_{i=1}^m \sum_{k=1}^n \frac{c_i a_{ijk} p_j p_k}{V_i}}$$

where $V_i = \sum_{j=1}^n \sum_{k=1}^n a_{ijk} p_j p_k$, the mean viability in the i th niche.

Writing $V = \sum_{i=1}^m V_i c_i$ we obtain

$$p_j' = \frac{p_j \partial V / \partial p_j}{\sum_{j=1}^n p_j \partial V / \partial p_j} \tag{1}$$

Equation (1) is essentially equivalent to that studied by Baum and Eagon⁷. They demonstrated that $V' \geq V$, with equality only at an equilibrium of the system, that is, when $p_j = p_j'$ for all j . Thus the fitness function V increases from generation to generation. In this case V is considerably more complicated than in the single niche problems, and the possibility arises of several equilibria or of continuous curves of equilibria existing⁶.

We should note that all the cases of increasing fitness mentioned above, and also the p -sex model case of Blakeley⁸ are direct, or indirect, consequences of the same theorem⁷. All these models have certain basic features, first, random mating amongst the whole population, and second, identical viabilities for the two sexes. The addition of extra complexity such as inbreeding, differential selection for males and females, or asymmetry of genetic system destroys the property of increasing V .

Finally we note that the various systems with increasing V can be combined; V will increase for selection with n alleles, m niches, k loci with additive fitness for loci, and p sexes.

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- ¹ Mandel, S. P. H., *Heredity*, **13**, 289 (1959).
- ² Mulholland, H. P., and Smith, C. A. B., *Amer. Math. Monthly*, **66**, 673 (1959).
- ³ Kingman, J. F. C., *Proc. Camb. Phil. Soc.*, **57**, 575 (1961).
- ⁴ Ewens, W. J., *Nature*, **221**, 1076 (1969).
- ⁵ Levene, H., *Amer. Naturalist*, **87**, 331 (1953).
- ⁶ Cannings, C., *J. Genetics*, **60**, 255 (1971).
- ⁷ Baum, L. E., and Eagon, J. A., *Bull. Amer. Math. Soc.*, **73**, 360 (1967).
- ⁸ Blakeley, G. R., *J. Theoret. Biol.*, **17**, 252 (1967).

Depression of Yield in Ryegrass Exposed to Sulphur Dioxide

PREVIOUS work¹ has shown that substantial economic losses may occur when S23 ryegrass is grown in areas of high coal-smoke pollution. Evidence suggested that sulphur dioxide was the toxic factor producing the depression in yield, although this could not be proved. We decided to investigate the effects of prolonged periods of low SO₂ concentration on the growth of S23 *Lolium perenne* in order to establish whether SO₂ can cause invisible injury and also to measure the depression of yields at different concentrations of the gas. We also used clones of wild *L. perenne* collected from Helmsore in a polluted region of East Lancashire. Observations at the ADAS Experimental Husbandry Farm at Helmsore have indicated that the native ryegrass in the district is apparently tolerant to the polluted atmosphere (C. H. Mudd, personal communication).

We grew the plants in bowls inside two Perspex chambers situated in an open-sided greenhouse. The chambers were ventilated with the ambient air, which was purified by passage through activated charcoal, followed by an absolute filter. A controlled uniformly distributed concentration of sulphur dioxide was maintained in one chamber, by bleeding SO₂ at a controlled rate into the air inlet pipe. The plants were grown in a well fertilized brown earth, watered by sub-irrigation.