

## GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS OF Papers read at the HUNDRED AND TWENTY-NINTH MEETING of the Society, held on 19th and 20th March 1959, at the UNIVERSITY OF BIRMINGHAM

### POLYPLOIDY IN WHEAT

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There are only bivalents at meiosis in the hexaploid bread wheat, *Triticum vulgare*, although its three genomes are derived from cytologically related diploid species and equivalent chromosomes of the three genomes are genetically very similar, as has been shown by nullisomic-tetrasomic compensation. Thus wheat has acquired a diploid form of meiotic behaviour in which the pairing affinity between equivalent chromosomes in different genomes either no longer occurs or is no longer expressed. The diploid behaviour is controlled by a gene, or genes, on one chromosome, in the absence of which intergenome pairing takes place and wheat ceases to behave as a classical autosyndetic allopolyploid.

Evidence of the localised genetic control of a purely bivalent forming regime makes possible a simplified concept of evolution of polyploidy, and may influence attitudes to some practical breeding problems.

### REVERSIONS OF THE LEUCINE AUXOTROPH LEU-151 OF SALMONELLA TYPHIMURIUM

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“Reversions” of the leucine auxotroph *leu-151* of *Salmonella typhimurium* to leucine independence are of three types, fast, slow and unstable, distinguishable by their growth in the absence of leucine. The fast growing type is probably due to a back mutation of *leu-151* to *leu+*. The slow type has been shown by transduction tests to be due to a suppressor mutation, (*su-leu*) at a locus which is linked to *leu-151* and to *ara-9*. This suppressor is allele specific in that it has no effect in combination with *leu-39*. A linkage map of the region has been plotted and the order of the markers shown to be *su-leu*, *leu-151*, *leu-39*, *arg-9*. The unstable type, also slow growing, spontaneously reverts to auxotrophy at a very high rate. The instability has been shown not to extend to the *methionine A* and *tryptophane B* loci, in that the mutation rates of *me A-22* and *try B-2* to prototrophy are unaffected.

### INDUCED MUTANTS IN COPRINUS LAGOPUS

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Some 250 mutants have been isolated in *Coprinus lagopus* following ultra-violet irradiation of oidia. The mutants obtained were largely biochemical with the greatest proportion showing requirements for adenine and methionine. Those requiring amino acids, vitamins and purines (excluding adenine and methionine) were less frequent. Several methods of mutant isolation were tested. The transfer of colonies from seeded plates to complete slants before testing to minimal medium appeared to give a better result than testing colonies directly to minimal medium

and rescuing non-growers (auxotrophs) to complete medium. The total isolation method produced a yield of approximately 1 per cent. mutants among survivors whilst filtration enrichment doubled this figure. Thirty-six auxotrophic and seven morphological mutants have been tested for linkage with the mating type loci. Ten of the auxotrophs are lined with the *A* locus and include mutants with requirements for methionine, paba and arginine. Four responding to choline are linked with the *B* locus. They fall into three groups when tested on intermediates in choline synthesis. In conjunction with Dr P. R. Day tetrad analysis of two *A* and three *B* linked markers was used to determine their linear order and their position in relation to the centromere.

## THE EFFECT OF RANDOM FLUCTUATION ON GROUPS OF RAPIDLY EVOLVING POPULATIONS

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By use of high-speed computation techniques, an analysis has been made of the Sewall Wright effect in rapidly evolving populations, which do not seem to be amenable to direct statistical treatment. The effect is shown to be considerable even in large populations. The principle is extended to investigate the effect of random fluctuations on gene flow between populations, and its effect in determining population pattern. Primrose populations containing homostyle plants are chosen as the models for this investigation.

## SOME GENETIC EXPERIMENTS WITH STERNOPLURAL ASYMMETRY IN *DROSOPHILA*

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Left-right asymmetry of sternopleural bristles in *Drosophila* provides perhaps the most recondite character in the current repertory of quantitative inheritance. Dismissed, on the one hand, as manifestations of "developmental noise" (by analogy with information theory), variations in the level of asymmetry have also been interpreted as a "useful measure of developmental homeostasis". Of particular interest is the fact that the level of asymmetry is at least partially under genetic control, since it was reduced when two inbred lines were crossed, and responded to selection from the  $F_2$ . This appears to form a striking contrast with the behaviour of the "antero-posterior asymmetry" of bristle number on the abdominal sternites, which is not easily affected genetically.

Experiments to be described indicate that two wild stocks of *D. melanogaster* both had a small but significant genetic variance for sternopleural asymmetry, and provide further data on the effects of crossing homozygous lines. In the light of these experiments some difficulties in interpreting the behaviour of the character will be examined.

## COUPLING AND REPULSION LINKAGES UNDER DISRUPTIVE AND STABILISING SELECTION

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Two lines of *D. melanogaster* have been maintained for seventeen generations, one under disruptive selection with negative assortative mating, the other under stabilising selection. Both were initiated from the same  $F_1$  cultures of a cross between a *vg/vg* high sternopleural chaeta number line (mean 40 chaetae) and a *se cp e* stock

(mean 15 chætæ). It was known that important differences affecting chætæ number occurred in the *se cp* region of chromosome III. Selection (1 in 20) began in F<sub>2</sub>. Flies were selected for chætæ-number: no selection for marker phenotypes was exercised.

Stabilising selection reduced variance from F<sub>2</sub> level (30) to approximately F<sub>1</sub> level (5). *vg*, *e* and *cp* were largely eliminated, and the majority of the third chromosomes in the line became *se* +.

Disruptive selection stabilised variance at a level roughly midway between that of F<sub>2</sub> and that of F<sub>1</sub>. The line became homozygous *vg* and *e* but established a testcross system  $+ +/se\ cp \times se\ cp/se\ cp$ . It could be shown that + and *se* were linked with genes with strong effects on chætæ number, and that recombination was continually breaking down the coupling linkage of these genes, and the linkage of some of them at least to the *se* locus.

The experiment therefore demonstrates that disruptive selection can maintain coupling linkages of relevant genes against considerable "recombination pressure" and that stabilising selection can promote repulsion linkages.

The disruptive selection line, at the end, was polymorphic for the loci *se* and *cp*, and gave a strongly bimodal distribution for chætæ number.

## GENE-ENVIRONMENT INTERACTION IN THE GROWTH OF *DROSOPHILA*

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The problem of genetic differences in ability to withstand a deficient diet during larval growth in *Drosophila* has been studied by rearing flies on chemically defined aseptic media in which the general nutrient concentration is varied or the amino-acid supply is restricted. Performance, measured by the relative decline in adult body size compared with growth under the most favourable conditions, may be regarded as an important constituent of fitness. Tests have been carried out on inbred lines, strains selected for large and small body size and on various crosses between them. They suggest a fairly systematic tendency for departure from the original mean in either direction to be associated with progressive loss of resistance to sparse diets and this can be detected after only a few generations of mass selection. Since the environmental conditions are repeatable, it should be possible to place these relations on a more systematic, quantitative basis.

## SOME GENETIC IMPLICATIONS OF MATERNAL EFFECTS

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In a crossbreeding experiment involving all types of matings among Friesian, Ayrshire, and Jersey cattle, the effect of maternal size has been investigated, based on various comparisons of reciprocal crosses, using data on weight and body size from birth to two years of age. Among the thirteen characters analysed, there was a close relationship at birth between the relative maturity of the characters and the relative extent of their maternal effects. The type of maternal effect depended on whether the crossbred calf is from the larger or smaller maternal breed, but in all cases the effect diminished during the calf's growth. The information will be interpreted in terms of variation in expression of the genotype for body size from birth to maturity. The main conclusions will indicate how an understanding of maternal effects might facilitate a selection programme by permitting selection to be carried out at an early age.

## MATERNAL AND SEX-LINKED EFFECTS ON GROWTH AND FORM IN THE FOWL

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C and I are inbred lines of White Leghorn ( $F \sim 99$  per cent.).  $C \text{♀♀}$  weigh approximately 1600 g. at sexual maturity and  $I \text{♀♀}$  1300 g. The  $F_1 I \text{♂} \times C \text{♀}$  is heavier in both sexes at all ages than the reciprocal cross; average weights of  $\text{♀♀}$  at sexual maturity are:  $I \times C - 1670$  g. (171 days);  $C \times I - 1540$  g. (169 days). In  $\text{♂♂}$  (homogametic sex) the difference between reciprocals is smaller, and crosses of  $F_1 \text{♀♀}$  with  $\text{♂♂}$  of a third inbred line support the view that about one-third of the difference between reciprocal  $F_1 \text{♀♀}$  is due to sex-linkage, the smaller (I) line having the "larger" X-chromosome.

Despite their lower body weight,  $C \times I \text{♀♀}$  are identical with  $I \times C \text{♀♀}$  in mean length of tarsometatarsus and slightly exceed them in thickness of shaft of tarsometatarsus (measurements on dried bones of  $\text{♀♀}$  killed at 490 days of age). Skeletal dimensions, as well as body weight, are subject to hatch effects, but may change in opposite directions from one hatch to another. Thus differences between hatches as well as between reciprocal  $F_1$ 's reveal changes in conformation as well as size. The interpretation of these changes in terms of relative growth-rates will be discussed.

## SPONTANEOUS MUTATIONS IN DRY *NEUROSPORA* CONIDIA

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Atwood's heterocaryon for the scoring of recessive lethals was used in an attack on the problem whether spontaneous mutations arise in non-duplicating genes. This method, in contrast to previous ones, detects only mutations which arise before plating, and excludes those which arise on the plate through replication errors. The results show that lethals arise at a constant rate in dry conidia. Under the conditions used, this rate was 0.3 per cent. per week at  $32^\circ$ , and considerably lower at  $4^\circ$ . When spores kept at  $32^\circ$  were transferred to growth medium, a high proportion of the already present lethals was lost during the initial establishment of a growing front; subsequently, mutation frequency increased at about twice the rate found for dry conidia. A spore sample which had spent the first six months at  $4^\circ$  and the seventh at  $32^\circ$  contained at least as many lethals as spore samples which had been kept at  $32^\circ$  throughout. If this result can be confirmed, it suggests the existence of a two- (or multiple-) step process, with only the final step showing marked temperature dependence.

## POLYGENIC MUTATIONS AFFECTING VIABILITY

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Data on the viability of irradiated X-chromosomes of *Drosophila melanogaster*, summarised in a paper by Luning and Jonsson (1957), have been analysed in an attempt to determine the characteristics of "normal" treated chromosomes, that is, after the exclusion of lethals and semi-lethals. The most definite effect is a reduction of mean viability of males with treated chromosomes relative to the controls. This is highly significant statistically. At first sight all chromosomes appear to be affected uniformly: there is no suggestion of bimodality, not even of increased variance. After applying some corrections, however, there appears to be a slight increase in variance of treated chromosomes. As far as it is possible to judge from the published

material, the data appear to be very similar to those earlier obtained by Timoféef-Ressovsky (1935) and Kerkis (1938). It is the interpretation which is different : that the results are due to very small mutations of very high incidence, such that after 2000  $r$  to mature sperm, the incidence of mutations is greater than one per chromosome.

## A MODEL FOR RECOMBINATION BEFORE ZYGOTENE PAIRING

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Recombination by copy-choice requires homologous contact between chromosomes at the time of replication. In apparent contradiction to this, replication of DNA occurs before zygotene pairing in a number of organisms.

In *Aspergillus* and other organisms, only a small fraction of the total genetic length is available for recombination to take place in any one cell. The necessary condition for recombination is called effective pairing to distinguish it from cytologically observable pairing. In *Aspergillus*, effectively paired segments have a mean length of about 0.4 map units and the mean exchange frequency per segment is 0.6. This corresponds to a recombination fraction of 35 per cent. and means that the frequency of recombination between loosely linked loci is determined principally by the frequency of effective pairing between them ; effective pairing is a limiting factor in recombination.

If effective pairing were equivalent to homologous contact, chromosomes need be in contact at only a few points at the time of recombination to account for their genetic length. There need be no cytologically observable pairing. There is no direct evidence that effective pairing is equivalent to homologous contact, but if it were, the well-known observation that chiasma frequencies are greater in triploids and trisomics than in the corresponding diploid might be accounted for in terms of increased probability of homologous contact between pairs of chromosomes when three are present as compared with two.

## ALTERNATIVES TO HETEROSIS

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The diversity of the blood groups in man and other vertebrates lies within Ford's definition of polymorphism, and heterosis is a sufficient mechanism for the development and maintenance of this variability. Although it is sufficient, it is not necessary and in view of the absence of any unequivocal evidence of any specific heterotic advantage in any serological character various other explanations will be considered.

Opportunities for the expression of differential fitness of various genes may occur through selective mating, selective gamete conjugation, maternal-foetal interactions, and differential morbidity after birth. Maternal-foetal interactions, while undoubtedly complicating the situation, cannot explain it as the evolution of serological individuality preceded placentation.

In particular it will be maintained that :

- (1) Inbreeding depression associated with a variable amount of inbreeding will lead to the perpetuation of many forms of genetic variability, not all of which need contribute to increased vigour on outbreeding.
- (2) A tendency for gametes with dissimilar surface properties to conjugate preferentially will lead to an extremely stable variability if these properties are determined by the gametic genotype. This selection may or may not be of any biological significance in the viability of the diploid organism.

A MUTABLE GENE IN *DELPHINIUM AJACIS*

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$p$  (pink),  $p^b$  (blue),  $p^l$  (lavender) and  $p^*$  are alleles at a locus controlling flower colour.  $p^*$  mutates at a high rate to  $p^b$  and to an allele which has a low rate and complicated pattern of mutation to  $p^b$ . The rate of mutation of two doses of  $p^*$  to  $p^b$  is twice the rate of mutation of one dose of  $p^*$ , in both the sepals and the reproductive tissues.  $p^*$  has a high mutation rate only when a dominant activator gene is present.

The inheritance of mottled pink/rose flowers and mosaic green/yellow leaves will also be discussed briefly.

## DIFFERENTIATION IN THE POTATO TUBER

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Tubers of the cultivated tetraploid potato (*Solanum tuberosum* L.) may have anthocyanin pigments in the cells of either the periderm or the outer cortex. The results described here are for pigmentation in the periderm, which in potato tubers is formed nearly entirely from the epidermis.

When eyes were removed from the white-splashed-purple tubers of a seedling so that adventitious buds were produced from the inner tissues, some of the resulting plants had white tubers. Clonal generations from the original white-splashed-purple tubers and from the white tubers obtained by the eye-excision experiment have remained true to their respective types.

Hybrid progenies from crosses of white tubered varieties on to the plants with white-splashed-purple tubers and on to the plants with white tubers both showed similar segregations of approximately 11 white-splashed-colour : 13 white.

The simplest explanation of these results would appear to be that the cells of the inner tissues of a tuber differ from those of the epidermis (and the periderm which it produces) in not being able to produce the purple pigment, and that they do not regain this power even when they are made to become epidermal cells and even although their nuclei contain the gene for white-splashed-colour periderm.