

GENETICAL SOCIETY OF GREAT BRITAIN

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EXPERIMENTS ON THE INDUCTION OF MUTATIONS IN CROP PLANTS

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Experimental work on the use of P^{32} as a mutagen on various species of crop plants is presented. The distribution of radio-activity in various parts of the plants has been measured and the biologic half-life of the isotope was found to be substantially less than its physical half-life owing to exudation through the roots.

Mutant phenotypes identical with those existing in wild populations were recovered. These were characterised by differences in growth rate as compared with both the wild type and the naturally occurring mutants. Evidence is presented which indicates that the variability of complex quantitative characters is increased in irradiated material, and that selection for maximum character expression is therefore made more effective.

THE USE OF ARTIFICIALLY INDUCED MUTATIONS IN CROP IMPROVEMENT

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Plant Breeders are facing a challenge from the claims made for mutation breeding. They must decide what should be their response to this new method. An attempt will be made to analyse the problems confronting the breeder who wishes to use mutagenic agents for crop improvement. The techniques involved will be considered with reference to self-pollinated, cross-pollinated and vegetatively propagated plants.

It is suggested that in the present state of our knowledge, mutation breeding is of very limited value but that there is need for much more fundamental work on the mutation process.

CYTOPLASMICALLY DETERMINED VARIATION IN *ASPERGILLUS NIDULANS*

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Strains of *A. nidulans* carrying nutritional markers and also resistant (single gene determined) to acriflavine undergo irreversible changes after serial subculture on medium with acriflavine. Controls without acriflavine are unchanged. Three such modified strains have so far been studied. They bear few or no conidia and are described as "mycelial". They are stable on repeated subculture on any medium so far tested, with or without acriflavine. The mycelial condition is cytoplasmically determined and can be transmitted infectively to other genotypes (with or without

an allele for acriflavine resistance) by heterokaryosis. Nucleo-cytoplasmic interactions are pronounced and each mycelial cytoplasm gives a wide range of phenotypes in combination with different genotypes. The three original mycelial strains have been shown to be cytoplasmically different by combining each cytoplasm with a common genotype; the three strains so obtained were phenotypically quite distinct. Heterokaryotic combinations of pairs of mycelial cytoplasm do not restore the non-mycelial type.

Balanced heterokaryons (and heterozygous diploids derived from them) between a mycelial and a non-mycelial type are almost normal suggesting that the mycelial condition is little expressed in a prototroph. However, mitotic recombination in such diploids gives types of which a proportion are mycelial. Meiotic recombination in crosses between a mycelial and a non-mycelial gives both mycelial and non-mycelial types. Preliminary results suggest that segregation of the mycelial condition at meiosis is irregular. At mitotic recombination in heterozygous diploids the determination of a mycelial versus a non-mycelial phenotype appears to be closely correlated with the particular genotype produced at crossing-over or haploidisation. That is, certain genotypes appear always to express the mycelial phenotype while other genotypes express the non-mycelial phenotype.

UNEXPLAINED RESPONSE OF MICE TO SELECTION FOR LACTATION

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Selection for lactation in mice has been carried in both upward and downward directions through 20 generations. A number of reverse selections, made in parallel with the two forward lines, helped to assess the magnitude of heritable variation within the lines. The divergence for each generation between the progenies of forward and reverse selected parents indicated that heritability was one-half and did not change during the experiment. Nevertheless, the rate of divergence between the two forward selected lines declined in successive generations so that, by the 20th, only one-sixth of the total forward selection applied was realised as a difference between lines. Thus, on average, a five-fold change in response followed a change in the direction of selection.

Two plausible explanations of these results failed to stand up to tests. Natural selection was excluded because, when artificial selection was relaxed, fitness did not improve. Maternal effects were excluded because hybrids reared by high line mothers had identical lactations to their reciprocals reared by low line mothers. In default of these mechanisms the results remain unexplained.

AN EFFECT OF THE UTERINE ENVIRONMENT UPON SKELETAL MORPHOLOGY IN THE MOUSE

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Maternal effects upon body size have long been known in horse-donkey hybridisation, and more recently demonstrated in Walton and Hammond's classical Shire-Shetland crosses. Green and Russell observed a maternal effect in mice involving the axial skeleton. Reciprocal hybrids between two inbred strains of mice, having predominantly five and six lumbar vertebræ respectively, showed a difference in number of lumbar vertebræ in the direction of the maternal strain. We have confirmed this finding, and have shown by means of egg transfer that the maternal effect is mediated through the uterine environment provided by the mother rather than through the egg cytoplasm. Number of lumbar vertebræ is not related to body size, hence the influence exerted by the uterine environment is presumably not a simple nutritional one.

THE SPREAD OF GENES IN A CLOSED POULTRY FLOCK UNDER SELECTION

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It has been said that a fit individual will leave descendants many generations after its death. Fitness in this sense is the result of natural selection while in a selective programme fitness is also attached to the character under selection. The spread or decrease of an ancestor's genes may be detected by pedigree studies for a few generations after which changes still occur due to selection but these cannot be detected from pedigrees.

It is possible to partition these changes in the frequency of ancestors' genes into changes due to natural and artificial selection.

The results of such a pedigree analysis in a flock of domestic poultry under selection for egg production led to the conclusion that the response to selection may have been improved if assortative mating had been practised in conjunction with selection.

HYPOPHOSPHATASIA, EXCRETION OF ETHANOLAMINE PHOSPHATE IN CLINICALLY NORMAL RELATIVES

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Hypophosphatasia is a rare osteodystrophic disorder. Biochemically it is characterised by a marked reduction in the level of serum alkaline phosphatase activity and a greatly increased excretion of ethanolamine phosphate in the urine.

The families of 14 individuals presenting with this condition have been investigated. No instance of parental consanguinity was observed. Out of 13 sibs of the propositi, two were diagnosed as having hypophosphatasia. No cases of the disease were found among other close relatives. Slight but definitely abnormal levels of ethanolamine phosphate excretion were observed in the urine of some members of the families. It is suggested that the clinically affected individuals are homozygous for a rare gene which in the heterozygotes leads only to a minor biochemical abnormality. If so, about 60 per cent. of the presumed heterozygotes can be detected by the chromatographic methods used.

The severity of the disease and the age at which the osteodystrophy becomes apparent are very variable. In our own, and in published material, sibs resemble each other rather closely in these respects. This suggests that more than one gene may be involved. Further heterogeneity in the material is revealed by the fact that the heterozygous manifestation rate is different in different sibships.

VARIATION IN THE J CHARACTER OF CATTLE BLOOD

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The J character is a well known antibody-antigen system in cattle. Blood samples from a population of twin cattle have been tested for both J antigen and J antibody, the presence of the one confirming the absence of the other.

Variation in J antibody titre in time occurs, but the causes are not known. Twin studies show that the antibody first appears at about six months of age (except perhaps when transmitted in colostrum) and the titre is highest in autumn. Titres are commonly depressed about the time of calving.

J antigen strengths vary between individuals, but are identical within sets of one egg twins. Among adults, the order or rank of antigen strengths remains constant. Both antigen and antibody are independent of erythrocyte mosaicism

and therefore the J antigen has a value in twin diagnosis. With the aid of the knowledge that the J antigen varies genetically in strength, it is now possible to demonstrate sometimes a genetic difference between twins that are both J positive.

THE LINEAR GROWTH PROCESS IN TWIN CATTLE

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Growth is studied in two populations of twin cattle belonging to the Animal Breeding Research Organisation; one population is comprised of 60 monozygous twin pairs, and the other of 60 dizygous pairs.

The data consist of regular observations up to an age of 2 years on several linear body measurements.

A study of the population growth curves suggests a simple stochastic representation for the linear growth process.

Variation and co-variation in the linear growth of twin and co-twin are analysed in the light of this hypothetical process.

A large part of the variances and co-variances within twin pairs are explained in terms of a population growth constant.

RYE-WHEAT CHROMOSOME ADDITION AND SUBSTITUTION LINES

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Characteristics of rye, *Secale cereale*, cannot be transferred to wheat, *Triticum vulgare*, by normal breeding methods because there is no meiotic pairing between the chromosomes of the two species in interspecific hybrids and amphidiploids. Therefore to introduce rye characters into wheat, in balanced combinations, with the least disturbance of the wheat phenotype, single pairs of rye chromosomes have been added to the full chromosome set of wheat. Separate single-pair addition lines for five of the seven different rye chromosomes have been obtained by back-crossing and selfing derivatives of wheat-rye hybrids and amphidiploids. Each rye chromosome produces a distinctive modification of the phenotype of wheat, and useful characteristics such as disease resistance, are introduced with some chromosomes. Addition lines differ in fertility and stability.

Lines have also been developed which have telocentric derivatives of rye chromosomes, either as monosomic, or disomic additions. These lines permit the extension of the genetic information obtained from whole chromosome additions.

In the derivatives of crosses of disomic addition lines with wheat monosomics, lines have been extracted in which a wheat chromosome pair has been replaced by a rye pair; the chromosome number remaining at that of wheat. The rye pair adequately compensates for the absence of the wheat pair, in the few lines so far examined, and the distinctive phenotype of the addition lines is largely retained.

CYTOGENETIC STUDIES WITH ANEUPLOIDS IN COMMON WHEAT

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Genetic analyses of qualitative and quantitative characters in wheat have been conducted with aneuploids and special lines derived from them.

The study of nullisomics and monosomics in Chinese Spring wheat and of F_1 , F_2 and F_3 progeny from crosses between these lines and varieties with contrasting

characters has resulted in identifying the chromosomes that carry genes for awning, growth habit, seed coat colour, leaf rust reaction, stem rust reaction, spike density, etc. Changed character expression of F_1 in some instances, and F_2+F_3 ratios modified by characteristic univalent chromosome transmission and breeding behaviour, revealed the critical chromosome(s).

Substitution lines, that is 21 lines in which the 21 chromosomes of a variety are each replaced by the homologue from a donor variety have been used to study disease reaction, awning, earliness, lodging resistance, height yield, etc. Since each substitution chromosome is present in the genetic background of the recipient variety, and since these studies can be conducted in well replicated field trials, the genetic effect of each chromosome on the character studied is clearly expressed and can be statistically measured.

Examples to illustrate these situations are presented and a brief account of new studies is given.

GENETIC VARIATIONS IN THE RESISTANCE OF SHEEP TO INFESTATION WITH ROUNDWORMS

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Nematode worms of various genera inhabit particular regions of the sheep's intestine, and cause damage which forms an important economic problem. The faecal egg count, to which worms of several genera contribute eggs of identical appearance, is a widely used index of the level of infection, and the only one available from the live sheep. In hill sheep, this index generally rises sharply to a peak in the spring, following the poor winter diet, and falls off in summer and autumn as the condition of the hosts improves. This indicates that environmental conditions have a marked effect on the faecal egg count, and also that sheep can build up a considerable degree of immunity to infection, which is impaired by malnutrition. The paper will describe an attempt to disentangle some of the factors contributing to the phenotypic variance in egg count, and to determine whether there are appreciable genetic variations in the ability to resist infection.

A SUPPRESSOR OF CITRULLINE DEPENDENCE IN *NEUROSPORA*: A CASE OF SINGLE GENE HETEROSIS

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A citrulline-dependent strain (33442, or *cit*) of *Neurospora crassa* has been used to study reversion to independence. In such mutation experiments plating is done on media supplemented with lysine and canavanine to eliminate leakage. In one experiment where plates were supplemented also with hydrolysed RNA, mutant colonies which were citrulline-independent but pyrimidine-dependent were found unexpectedly. They probably stemmed from one spontaneous mutant clone.

Both *cit* and the pyrimidine requirement are closely linked to the colonial marker *co*, yet the two requirements are not allelic. Crossing *co* pyrimidine-dependent with *co+* prototroph, most of the *co* pyrimidine-independent segregants are citrulline requireers. This suggests a map order: *co-cit-pyr* (*pyr* could be allelic to the previously known *pyr₃*), where *pyr* suppresses the *cit* phenotype. It is not possible at this stage to discriminate between suppression due to *pyr* taking over the synthesis of citrulline, or due to less direct metabolic interactions as have been suggested by Mitchell and Mitchell for other interrelations between pyrimidine and arginine mutants.

The *cit* and the *cit*, *pyr* nuclei combine to make a heterokaryon able to grow on minimal medium. This is an example of overdominance, since both nuclei differ by only one mutation.

HYBRID VIGOUR OF F₁ MICE AT LOW ENVIRONMENTAL TEMPERATURE

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Mice of strains A2G and C57BL, and first generation hybrids from these strains, have been bred at two environmental temperatures: -3°C . and 21°C . (controls). Fertility was higher in the hybrids than in either of the parental strains. The difference was greater at the low temperature: for instance, the mean number of young weaned by hybrid pairs was about twice as great as by inbred pairs at 21°C ., about five times at -3°C . Heterosis was shown also in the weights of the young of the hybrid pairs. Variability, especially in breeding performance at -3°C ., was much lower in the hybrid than in the inbred mice. Young hybrid mice, transferred from 21°C . to -3°C . were more resistant to the cold than young inbred mice.

EFFECTS OF TEMPERATURE, AND OF SELECTING RARE CROSS-OVERS, ON RECOMBINATION IN *ASPERGILLUS NIDULANS*

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When recombination frequencies are measured in that small proportion of all meiotic products in which there has been crossing-over between two very closely linked markers, it was shown by Pritchard in *Aspergillus* and by Doermann in bacteriophage, that recombination in regions adjacent to the selective markers is higher than in the whole population. I have now found, in addition, that when rare cross-overs are selected recombination in a region on the same chromosome as, but not adjacent to, the selective markers may or may not be increased. The occurrence or otherwise of this increase depends on the positions where crossing-over occurs in the chromosome, a distribution which varies with temperature (cf. *Drosophila*). There is no evidence of an effect of this kind when recombination is measured in different chromosomes from that carrying the selective markers.

FURTHER EFFECTS OF DISRUPTIVE SELECTION

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Since the previous report it has been confirmed that lines exposed to Disruptive selection possess considerable free genetic variation and that the line maintained under Stabilising selection (Mather's terminology) possesses much less. In addition, the line maintained under disruptive selection with positive assortative mating has produced striking results. This line has two components in different cultures, one with parents selected for high chaeta-number and the other with parents selected for low, but in each generation all offspring are produced by hybridising the two components. There is in principle maximal (50 per cent.) gene-flow between the two components. (Random-mating would involve only 25 per cent. gene-flow.) Despite this maximal gene-flow, selection now maintains a consistent significant difference between the two components, though at first it did not. The population may therefore be said to have become essentially polymorphic (though not polymorphic by Ford's strict definition), and thus demonstrates that Mather was right in expecting disruptive selection to have polymorphism as one of its results. At the same time, considered as two sub-populations, the line shows that isolation is *not* a prerequisite for divergence. Twenty-five per cent. gene-flow is the maximum to be expected in nature and even 50 per cent. permits divergence

under divergent selection pressures. The demonstration that two adjacent populations of a species are genetically different, though it shows they are not one panmictic population, is therefore not unequivocal evidence that there is an isolation barrier between them.

GENETICS OF SEED GERMINATION DATE IN *PRIMULA VULGARIS*

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During some experimental work involving the germination within one greenhouse of seeds from sixteen different populations of primroses, it was noticed that there were striking and fairly consistent differences between the mean germination dates of seed from different populations, and in some cases between those of seed from different plants in a single population. These differences have now been shown to be controlled by nuclear genes, although the number involved is not known. The differences relate to temperature rather than to date; it is suggested that if, in natural conditions, there is an optimum date of germination common to all populations in an area, then if the optimum is generally achieved seed from the colder populations must be able to germinate at a lower temperature; with seed from the different populations sown and kept under identical conditions within one greenhouse, as spring temperatures rise the seed from the colder populations will be the earliest to germinate. The results obtained tend to support this view. The ecological and evolutionary significance will be discussed.

STATISTICAL PROBLEMS IN THE SELECTION OF CROP VARIETIES

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When plant breeders have produced a large number of new potential varieties of a crop, the best of these must be selected by field trial, rejecting those that have undesirable characteristics or low yields and preserving the highest yielders. Often such selection will be conducted in several stages, each stage consisting of field trials for one or more years on the basis of which some varieties can be rejected and others passed forward to the next stage. Questions then arise as to the optimal intensities of selection in different stages, the optimal division of available land or other measure of experimental resources between the stages, and even the optimal number of varieties with which to start and the optimal number of stages, in relation to the total increase in yield achieved. Statistical theory has been used to examine these questions for one relatively simple situation, and has suggested some simple rules as approximations to the best possible. The problem of relating the selection programme to the whole agricultural economy has also been discussed, one tentative conclusion being that a small number of stages and consequently a rapid testing and output of new varieties may often be preferable to more thorough and slower testing.

AN INVESTIGATION INTO THE GENETIC CONTROL OF YIELD IN SPRING WHEATS

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A 4×4 diallel set of spring wheat crosses was analysed in F_1 and F_2 by the method of Jinks and Hayman. The characters used were yield per plant and four components of yield, *viz.* weight per grain, number of grains per spikelet, number of spikelets

per ear, and number of ears per plant. The genetic control of the four components was found to be mainly by additive genes with very little evidence of dominance. There is a very slight indication of gene interaction in two of the components. Yield per plant showed strong evidence of gene interaction.

The use of this set of crosses to test the possibilities of this analysis as a tool in plant breeding will be discussed.

THE GENETIC STRUCTURE OF RYEGRASS STRAINS AND ITS IMPLICATIONS FOR HERBAGE PLANT BREEDING

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A difficulty in the improvement of many outbreeding crops is the heterozygosity of parent plants and the consequent release of variation during seed multiplication.

A survey has therefore been made of the amount of potential variation within two populations of perennial ryegrass (Irish and Kent) and of its rate of release under selection. The main character studied was date of ear emergence, which is highly heritable, and also shows good "repeatability" from year to year. Early and late selection lines were established, using different initial population sizes, and different intensities of inbreeding.

The results of the first three generations of selection are now available. Considerable response has occurred, even in the lines derived from a single individual, and the means of some of the extreme lines are well outside the range of the original populations. The use of four plants as the basis of selection in each generation has proved sufficient to avoid inbreeding depression.

Considerable potential genetic variation can evidently be carried within a small group of plants of similar phenotype, and rapidly released within a few generations. The implications of such a genetic structure in planning methods of selection and seed multiplication are discussed.