THE GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers presented at the HUNDRED AND EIGHTY-FOURTH MEETING of the Society held on 5th, 6th and 7th JULY 1977 at the University of Cambridge.

GENETIC STUDIES ON INTRASPECIFIC ANTAGONISM IN NATURAL POPULATIONS OF WOOD-DECAYING *BASIDIOMYCETES*

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Evidence that narrow dark zones in wood undergoing decay by several common basidiomycetes, including *Coriolus versicolor*, *Stereum hirsutum*, *Phlebia merismoides* and *Hypholoma fasciculare*, result from antagonistic interaction between adjacent individual mycelia of the same fungus species will be described. The implications of this phenomenon, notably in relation to previous concepts such as the formation of a genetically heterogeneous unit mycelium, will be explored.

Methods will be described for studying the genetic basis and significance of intraspecific antagonism in natural substrates by analysis of the 3-dimensional structure of populations within individual stumps and logs. Details of the results obtained so far will be presented.

PARTIAL SPINDLE OVERLAP AND GENETIC MAPPING IN *SORDARIA BREVICOLLIS*

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The use of ascospore-colour marker genes provides a very sensitive means of estimating the frequency of gene conversion, post-meiotic segregation, partial and complete spindle overlap in *Sordaria brevicollis*.

In view of the high frequency of partial spindle overlap in this organism, correction factors have been proposed for the estimation of centromere distances. The *y4* gene which nearly always segregates asymmetrically at the second division of meiosis has been assigned zero map unit on the assumption that all the asymmetrical ascal classes are illegitimate due to partial spindle overlap.

There is evidence that the *y4* gene though largely maintaining this characteristic segregation pattern also shows gene conversion and post-meiotic segregation indicative of recombinational events. The implications of these findings are discussed.

GENETIC ANALYSIS OF COURTSHIP SONG IN *DROSOPHILA MELANOGASTER*

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In the courtship of *D. melanogaster* the female remains relatively passive whilst the male performs a number of discrete activities including a wing display. The male extends one wing and vibrates it up and down for brief periods to produce patterned acoustic stimuli known as " courtship song ". This serves, as a species identification signal, and to stimulate the female to mate.

Males of an inbred strain derived from a wild population were found to be unusually unsuccessful in courtship compared with males of other inbred wild type strains, but this difference could not be explained in terms of variation in the performances of visible components of male courtship behaviour. The courtship song consists of two wave form elements known as sine song and pulse song Recordings of the song of the strain with low courtship

success show unusually high frequency sine song and pulse song, and an increase in the number of cycles in each bout of pulse song. Sine song is considered to be the component which lowers the threshold of acceptance of the female and its mode of inheritance has been studied. The sine song frequency is under the control of several genes located on the sex-chromosomes and on the autosomes.

BIOCHEMICAL GENETICS OF HISTIDINE AMINOTRANSFERASE (EC 2.6.1.38) IN THE MOUSE

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The effects of hormone induced levels of histidine aminotransferase on the concentration of histidine and the fluxes through its associated catabolic pathways have been studied in histidinaemic and normal mice. Variation in the activity of the histidine catabolic enzymes has been sought between inbred strains of mice. Mendelian segregation in the activity and heat stability of histidine aminotransferase has been observed and has been used to assess the identity of the isozymes in the cytosol and mitochondrion.

TESTING ASSUMPTIONS ABOUT THE CAUSES OF HUMAN DIFFERENCES

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In attempts to analyse the basis of human behavioural variation, four aspects are frequently the subject of untested assumptions: (i) the family environment; (ii) the additivity of genetical and environmental effects; (iii) the independence of genes and environment; (iv) the consistency of effects over sexes. Often simple data, such as those collected in most twin or family studies, will allow some of these assumptions to be tested.

WHENCE OUR OPINIONS?

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Three large twin studies of social attitudes were examined and gave consistent estimates of genetical, environmental and cultural components of variation. The contribution of assortative mating to between families differences is considered. Predictions were formulated on the basis of the twin data and tested using data on adopted families. The importance of cultural differences and the possible role of cultural transmission of attitudes from parents to offspring is discussed.

WHY ARE ABILITIES CORRELATED?

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Correlation between different measurements, each under partial genetical control, may be due to common genetical effects, shared environmental influences, or a combination of both. A similar breakdown may be made of the variance specific to each trait. These, and other more complex considerations may be specified in models for covariance structures which are multivariate extensions of the models discussed by Eaves and Last above. Maximum likelihood estimates of genetical and environmental components of common factor and specific variance are obtained and the goodness of fit of the model is tested by chisquare (Martin and Eaves, *Heredity*, *38*, 79-95).

The method is illustrated with twin data on cognitive abilities and personality measurements.

ESTIMATING THE NUMBER OF GENES IN A POLYGENIC SYSTEM BY GENOTYPE ASSAY

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A new method, genotype assay, for calculating k, the number of genes or more strictly effective factors responsible for a continuous variable, is described. The central feature is the determination of the proportion of individuals in the F_n generation of a cross between two pure breeding lines that are heterozygous at one locus at least, by an assay of their F_{n+2} grand progeny families. The observed proportion is then equated to a theoretical expectation which is a function of the number of genes involved. Expectations generalised to cover any generation n for experimental designs in which every F_n individual is assayed by comparing p F_{n+2} grand progeny families have been derived for four cases covering the whole spectrum of relationships between genotype and phenotype. They range from one extreme where it is assumed that all genotypic differences are expressed as phenotypic differences, to the other where as a result of internal and relational balance of genes only a fraction of genotypic differences are recognised. Data from a cross between varieties 1 and 5 of *Nicotiana rustica* are used to illustrate the new method and its superiority over all other procedures which are available for estimating k in all but a few exceptional species.

EYE PIGMENT POLYGENES OF *DROSOPHILA MELANOGASTER*

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The " wild type " ommochrome (brown) eye pigment of *Drosophila melanogaster* shows polygenic variation which is not simply a function of body size or crude eye dimensions. Since this pigment is the end product of a short biochemical pathway from tryptophan, which has been extensively studied using mutant variation, the system readily lends itself to an investigation of the type of variation which the polygenes are causing at earlier stages in the pathway. Substitution of different second chromosomes from wild populations are considered in terms of their effects on the pathway as a whole as well as simply at the level of the end product.

ALBINISM: A POLYGENE INFLUENCING MOUSE BEHAVIOUR?

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Polygenes have been studied in a number of ways including: the teasing out of individual polygenes or blocks of such genes from a convenient quantitative character by suitable breeding techniques: the construction of a polygenic character by combining major genes in a predetermined way, as was done by Wright in his studies of coat colour in guinea-pigs; and, as in this study, by examining the pleiotropic effects of a major gene on a quantitative character.

Albinism is a coat colour gene which has frequently been associated with genetic variation in various types of mouse behaviour. However, in many of the studies its effects have been confounded with other genetic variables, and the results are conflicting. New data on two sets of lines congenic for full colour, albinism, extreme dilution and pink-eyed dilution shows that the effect of the albino gene on open-field activity depends on the genetic background.

SYMPOSIUM: " THE NATURE OF POLYGENES "

Introduction: J. M. THODAY

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Genetic analysis of polygenic systems has and must depend heavily on the methods of biometrical genetics. Full understanding also requires concepts of the nature and action of the loci and alleles involved. Various authors have speculated on the nature of polygenes

and suggested among other things that heterochromatin, control genes, reiterated DNA may be involved, and some clearly think in terms of a different kind of genetic locus.

The question of the kind or kinds of locus involved can only be critically considered if segregation at particular loci which are components of a polygenic system can be separately studied. The results of some attempts to do this will be discussed and their implication for understanding of the nature of the genes concerned will be considered. It will be suggested that *any* kind of locus could contribute to polygenic variation.

POLYGENIC MODIFIERS OF WING VENATION IN *DROSOPHILA*: A MODEL SYSTEM

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Polygenic modifiers of wing venation in *Drosophila melanogaster* have provided an exceptionally clear system for analysing the genetic component of quantitative variation. Wing vein mutants allow one to measure phenotypic effects of polygenes influencing vein formation and to isolate individual polygenic loci. In such a system it has been possible not only to estimate the number of polygenic loci responsible for the differences among various selection lines, but also to begin studies of the precise developmental influences of the loci involved in quantitative variation. Several general conclusions can be drawn from these studies. First, as in studies of sternopleural chaetae number (*e.g.* Spickett and Thoday, 1966, *Genet. Res.*, *7*, 96-121) the majority of the genetic difference between strains can be accounted for by a relatively small number of polygenic loci. Second, vein length polygenes appear to produce their effects by modifying simple developmental processes that contribute to the formation of the complex phenotype (*e.g.* vein pattern) we observe in adults.

SOME SPECIFIC GENES AFFECTING QUANTITATIVE VARIABLES IN RODENTS

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Two strategies have been used to identify genes affecting quantitative aspects of hormonal function in rodents. In the first, the phenotypic metric is made more specific by refining the biochemical and physiological definition of the character. Such methods have been successfully used in the analysis of steroid production in mice and in studies of the cause of hypertension in selected lines of rats. An alternative approach has been to limit the amount of genetic variation affecting the character. This can be done in mice by investigating the differences between sublines of a standard inbred strain. Such investigations have been made, with interesting results, of the activity of the enzymes which make adrenaline and of the severity of diabetes mellitus. The considerable potential of recombinant inbred strains, made by inbreeding the F_2 of standard inbred strains, is being realized. They can be used to identify and locate genes affecting characters, such as susceptibility to environmental factors, which are difficult or impossible to measure on single animals.

When the genes affecting a quantitative character have been identified, it is important to study their interactions with each other, and with environmental variables.

THE LOCATION AND DESCRIPTION OF GENETIC FACTORS AFFECTING QUANTITATIVE VARIATION

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In the hexaploid bread wheat, the heritable variation for a number of quantitative characters has been partitioned into whole chromosome effects. In some cases this partitioning has proceeded as far as the location of single genetic factors. Two characters which have been studied extensively are flowering time and height, although grain yield and protein content have also received some attention. For some of these characters, almost all chromosomes have been shown to contribute to genetic variation. The more detailed studies of chromosomal and genetic factor effects have shown wide variations in their magnitudes.

Results suggestive of multiple-allelism have been obtained. Also, it has been possible to classify some of the genetic factors by their differing effects on component characters as well as by their differing environmental sensitivities.

The consequences of these findings to genetic analysis and plant breeding and also to physiological and developmental genetics are briefly mentioned.

GENETIC ANALYSIS AND THE CONTROL OF DEVELOPMENT OF HEIGHT IN WHEAT

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The dwarfing genes from the Japanese variety, Norin 10, have been used in world agriculture since 1961. It is only recently that attempts to determine the number and location of the genes involved have been successful. For many years their analysis has been hampered by the confounding effects of large numbers of segregating genes affecting height. Both conventional and aneuploid analytical methods have failed to resolve the problem. It was not until character analysis had shown that these genes for dwarfing conferred gibberellic acid insensitivity on plants that genetic analysis was able to proceed. This showed that the genetic system was simple and dwarfing was controlled by alleles at only two homoeologous loci, *Rht1* and *Rht2*.

Knowledge of the mechanism by which the genes, *Rht1* and *Rht2* operate has allowed predictions to be made concerning other quantitative traits that could be affected by the same genes. The ability to recognise the genes unequivocably has allowed the detailed investigation of these pleiotrophic effects. The effects of the Norin 10 genes on one such character, grain yield, and some implications of the effects for plant breeding are discussed.

GENETICAL AND PHYSIOLOGICAL ANALYSIS OF CONTINUOUS VARIATION IN FUNGI

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This review is based on studies in several fungal species, particularly *Aspergillus nidulans*, involving a range of characters, including radial growth rate and penicillin production. Independent isolates differ among themselves and the progeny of a cross between two such isolates typically shows a near-normal distribution for any continuous variable. The phenotypic range of the progeny and the results of selection experiments suggest that in the population as a whole, many (> 10) effective factors are involved for any particular variable (C. E. Caten and J. L. Jinks, *2nd Int. Symp. Genet. Ind. Microorgs.*, pp. 93, 1976). That a significant proportion of the genome can influence many variables is shown by the frequent pleiotropy of major markers and the high induction rate of continuous variation. Occasional crosses have revealed individual allelic differences with a major effect and, in one case, these have been related to a chromosomal locus (D. S. Cole *et al.*, *J. Gen. Microbiol.*, *96*, 423, 1976). In other crosses effective factors associated with marked chromosome regions have been detected.

Attempts to identify the components of continuous variables have highlighted the complexities and difficulties involved. For example, the difference between opposing selections for radial growth rate proved to be related to the distribution of cellular material, a little understood area of fungal physiology, rather than its rate of production. One analysis showed that factors removed from the immediate physiology of the character can have a marked effect. These investigations have emphasized that the distinction between major genes and polygenes is commonly operational rather than constitutional and that in many instances the same loci are involved.

POLYGENIC INHERITANCE IN BACTERIA

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When Demerec and his associates first studied the problem of bacterial resistance to antibiotics, they found several good examples of polygenic inheritance, showing either the

" penicillin pattern " (all first step mutations of small effect), or the " streptomycin pattern " (first step ranges from small effect to complete resistance) (*Ann. N.Y. Acad. Sci., 53*, 283, 1950).

Cavalli attempted a genetic analysis of such systems in *E. coli K12*, before the discovery of Hfr mating strains (*Heredity, 6*, 311, 1952; *Bull. World Health Org., 6*, 185, 1952). He concluded that several loci were involved in resistance to chloramphenicol and oxytetracycline, and that they might interact non-additively. Later, Reeve and colleagues continued the genetic analysis, with the aim of locating individual genes and studying the resistance mechanisms involved (*Genet. Res., 7*, 281, 1966; *11*, 97 and 303, 1968; *16*, 359, 1970). This work has been largely forgotten in the excitement over the streptomycin A locus and R factors, but it may contain some lessons for students of quantitative inheritance. Work in this field will be summarised, and it will be suggested that the mutations responsible for low level drug resistance are in fact minor mutations in essential genes concerned with membrane structure and function. Such " polygene " mutations may play a role in helping bacteria to adapt to their ever-changing environment.

VARIATION IN SATELLITE DNAS OF FIVE CLOSELY-RELATED SPECIES OF *DROSOPHILA*

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Quantitative and qualitative variation in highly repetitive (satellite) DNA of five closely-related species in the *melanogaster* species sub-group of the genus *Drosophila* (Sophophora), has been investigated. The phylogenetic relationships of these species have been previously established on the basis of chromosomal banding sequences (M. Ashburner and F. Lemeunier, 1976, *Proc. R. Soc. Lond. B., 193*, 137-157). Resolution of major and cryptic satellites has been possible with the use of preparative and analytical antibiotic density gradients. Differences in satellite DNA composition, between and within species, have been determined from buoyant densities and DNA/DNA hybridisations. Satellites have been found to be either specific to a species or common to several species. In general each species is unique in terms of the pattern of distribution of satellites, and the differences between species are related to the known phylogenetic relationships. These findings are discussed in the context of similar comparisons of the composition of repetitive DNA in other groups of closely-related species.

STUDIES ON THE LOCALISATION OF MALE SPECIFIC DNA IN THE HUMAN Y CHROMOSOME

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Digestion of satellite III DNA from normal human males with Hae III restriction endonuclease yields a fragment of DNA, 3700 nucleotide pairs in length, which is not detected in Hae III digests of female satellite III, but which can be identified in Hae III digests of total male DNA. The apparent specifity of this DNA to males suggests that it is so located on the human Y chromosome. We have tested for the presence or absence of this male fragment in DNA isolated from cells of individuals carrying various aberrant forms of the Y chromosome. These include Y chromosome variants with very small quinacrine bright regions at the distal ends of their long arms, a Y chromosome with the distal quinacrine bright region deleted and Y/autosome translocations carried in cells of phenotypically normal females.

Our studies on DNA isolated from these cells and DNA isolated from normal male and female cells suggests that some or all of the nucleotide sequence contained in the male specific fragment is found in female DNA, but with a heterogeneous spacing of the Hae III restriction site. The 3700 nucleotide pair fragment found in male DNA appears to be localised in the proximal non-fluorescent portion of the long arm of the Y chromosome, and in the most proximal part of the quinacrine bright fluorescent region.

GENETICS OF SEXUALITY IN THE GENUS *AGARICUS*

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The genus *Agaricus* has been little studied genetically although it includes the widely cultivated and economically important *A. bisporus*. Sexuality has so far been described in only two members of the genus, *A. bisporus*, itself, and *A. bitorquis* which is also grown commercially. Both species are unifactorial heterothallic. In *A. bisporus* the expression of this sexuality is extremely limited. By contrast, the four-spored *A. bitorquis* displays a distinct sexuality which is nearer to that expressed on the " classical " basidiomycetes, *Coprinus lagopus* and *Schizophyllum commune*.

We have shown two other species, *A. macrosporus* and *A. nivescens* to be unifactorial heterothallic. Sexuality in these two species is compared with *A. bisporus* and *A. bitorquis*.

The variation in expression of sexuality within the genes provides an insight into possible steps in the evolution of homothallism from heterothallism.

INHERITANCE OF AND THE EFFECT OF RECURRENT SELECTION FOR TIME TO FLOWERING IN *PHASEOLUS VULGARIS* L.

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In the analysis of variance of F_1 data from a 5×5 diallel crossing programme it was found that additive effects predominated for the time from sowing to first flowering. The narrow sense heritability estimate was 83 per cent and it was predicted that the date of maturity could be efficiently adjusted by selecting for time to flowering. In order to test these findings, selections of early and late flowering genotypes were taken from the F_2 generation of a biparental population. Early selections were intercrossed and also allowed to set selfed seed, and the same procedure was followed for the late selections. In the second generation further selections for lateness and earliness were taken from each population.

Greater advances occurred in the late selections than in the early selections, and reselection in the opposite direction was more successful in the late populations. The realized heritability was 85 per cent in the first generation which compared very closely with the estimate from the diallel analysis, but this figure declined sharply in the second generation. In the intercrossed populations, however, the realized heritabilities were considerably higher than in the selfed populations. There was evidence that the time to flowering was largely controlled by genes affecting growth habit characters, particularly main stem node number.

PHYSIOLOGICAL AND GENETICAL STUDIES OF THE ROLE OF LIGHT IN THE DEVELOPMENT OF THE MOSS *PHYSCOMITRELLA PATENS*

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Light plays an important role at a number of different stages in the development of *P. patens*. Spore germination shows an absolute requirement for light. In the dark, protonema consist almost entirely of caulonema which show strong negatively geotropic growth. In the dark, gametophores etiolate and grow negatively geotropically.

In the light, chloronemal proliferation is greatly enhanced and chloronemal growth is strongly positively phototropic. Caulonemal growth rate is lower than in the dark and caulonemata grow at right angles to the direction of light. Gametophores show strongly positively phototropic growth. In the light, no geotropic effects can be detected. There is evidence that all these protonemal and gametophore responses to light, as well as the detection of the absence of light to initiate the geotropic responses, are phytochrome mediated.

Various mutants which differ from the wild type in a number of responses have been obtained. One class has lost the phototropic responses of caulonema, chloronema and gametophores, but retains the other developmental responses to light. It therefore appears that the mechanisms mediating the phototropic responses of protonemal tissue must have at least one component in common with those mediating phototropism in gametophores.

THE ISOLATION AND ANALYSIS OF DEVELOPMENTAL MUTANTS OF THE MOSS *PHYSCOMITRELLA PATENS*

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The gametophyte of *P. patens* shows an ordered sequence of developmental events. Spore germination is followed by growth of the chloronema which in turn gives rise to the caulonema. Subsequently, gametophores are initiated on the caulonema. We have isolated many mutants affected in gametophyte development. These include several categories of mutants which are resistant to the auxin, α-naphthalene acetic acid, and several categories of mutants which are resistant to the cytokinin, 6-benzyl-aminopurine. We have devised selective procedures for isolating these classes of resistant mutants. Other developmentally abnormal mutants have been obtained by using the method of total isolation. Many of these mutants cannot be crossed sexually since they fail to develop gametophores. Therefore we are analysing them genetically by effecting parasexual crosses by means of protoplast fusion.

EVIDENCE FOR THE RESTRICTED PASSAGE OF GROWTH SUPPLEMENTS INTO THE SPOROPHYTE OF *PHYSCOMITRELLA PATENS*

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P. patens is a monoecious moss. Self-fertilisation occurs readily in the wild type and results in the production of sporophytes. We have isolated mutants which are auxotrophic for a variety of substances, including vitamins, amino acids and a purine. At levels of supplementation which allow vigorous growth of the gametophyte they are self-sterile but cross fertile in certain combinations. Progeny from crosses involving auxotrophic strains have been analysed and, in all cases, self-sterility has been shown to segregate as a pleiotropic effect of the mutations causing nutritional dependence. The fertility of some auxotrophs may be restored by increasing greatly the concentration of the appropriate supplement in the culture medium.

COMPLEMENTATION ANALYSIS OF AUXOTROPHIC MUTANTS OF THE MOSS *PHYSCOMITRELLA PATENS* USING PROTOPLAST FUSION

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Fusion of protoplasts from the moss, *P. patens*, was induced using polyethlene glycol. Protoplasts were isolated from six nicotinic acid auxotrophic strains of independent origin and fusion was induced in all possible pairwise combinations. Complementation was detected by the ability to recover hybrids able to grow without nicotinic acid supplement. On the basis of the results presented, three non-overlapping complementation groups were identified.

THE USE OF THE " L " CHROMOSOME TYPE FROM THE *PHYTOPHTHORA PALMIVORA* COMPLEX AS A MARKER

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In heterothallic species of *Phytophthora*, the initiation of sex organ formation depends upon the association of the complementary mating types, A^1 and A^2. Isolates attributed to

P. palmivora with distinctly different metaphase chromosomes have been observed. The " L " type has a basic number of 5 relatively large chromosomes; the " S " type has 10ca, much smaller chromosomes. The " L " type has been used as a marker in interspecific crosses. A drug-resistant A^2 mutant of *P. drechsleri* combined with an " L " type A^1 gave oogonia of both parental types. Thus the capacity of the drug-resistant type to produce oogonia had not been lost, as had been suspected.

By combining British isolates of *P. infestans* with A^1 and A^2 " L " isolates it was possible to obtain and identify sex organs of *P. infestans*, although, the A^2 alone did not react with *P. infestans*. It is believed that this is the first observation of meiosis in British isolates of *P. infestans*. Three isolates so far examined have about twice as many chromosomes as reported for Mexican isolates and are therefore tetraploid.

Information regarding the frequencies of selfed and hybrid gametangial combinations can also be obtained by using species with cytologically distinctive nuclei.

AN INTEGRATOR GENE IN *ASPERGILLUS NIDULANS*: REGULATORY AND METABOLIC ROLES OF ω-AMINO ACIDS

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The *int*A gene of *Aspergillus nidulans* meets the criteria for an integrator gene in the model for gene regulation proposed by R. J. Britten and E. H. Davidson (*Science*, *165*, 349, 1969). *int*A is a positive regulatory gene which, in a certain context, *viz*, the presence of ω-amino acids, " integrates " the expression of at least three probable structural genes (Arst, *Nature*, *262*, 231, 1976). The expression of at least one of these structural genes can be elicited independently of the others in another context, i.e. induction of acetamidase on the presence of amides. The three (unlinked) genes under *int*A control are *amd*S, specifying acetamidase, *gab*A, specifying a permease for ω-amino-*n*-butyric acid (GABA), and *gat*A, specifying a transaminase for GABA and other γ-amino acids. β-alanine is the best co-inducer for these three activities, but GABA is also effective. In contrast, β-alanine is a poorer substrate than GABA for the transaminase and is virtually not a substrate for the GABA permease. Expression of these three activities is constitutive in *int*A^c and uninducible in *int*A-strains. *gat*A-mutations lead to loss of transaminase activity whilst *gab*A- mutations lead to loss of GABA permease. A *cis*-dominant regulatory mutation tightly linked to *gab*A, designated *gab*I^c, leads to constitutive expression of GABA permease but only in the presence of a functional *int*A product.

A NOVEL REGULATORY MUTATION IN *ASPERGILLUS NIDULANS*

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The degree of expression of the tightly linked structural genes for nitrate reductase (*nia*D) and nitrite reductase (*nii*A) depends upon two positive control systems. The joint action of the *nir*A product, in the presence of the co-inducer (nitrate), and the *are*A product, in the absence of co-repressor (ammonium), effects enzyme synthesis (D. J. Cove, *Proc. Roy. Soc. B.*, *176*, 267, 1970, Arst and Cove, *Molec. gen. Genet.*, *126*, 111, 1973).

nis-5 is a regulatory mutation which maps in the *nii*A *nia*D gene region and leads to a low level of nitrite reductase activity which is independent of the two control systems. It weakly suppresses null mutations at both the *are*A and *nir*A loci, for nitrite utilisation. It has no effect on the regulation of nitrate reductase.

nis-5 reduces the maximal level of nitrite reductase attainable under fully induced conditions, leading to poorer than wild type growth on nitrite. However, no differences between nitrite reductase from *nis-5* and wild type strains *in vitro* have been detected.

No non-additive interactions have been detected between *nis-5* and various mutant, but not null, *nir*A and *are*A alleles in double mutants. There is thus no evidence that *nis-5* affects primarily a recognition site(s) for the *nir*A or *are*A product(s). We favour the hypothesis that the constitutive, derepressed component of nitrite reductase synthesis in *nis-5* strains depends upon a second promoter/initiator. How this has come about will be discussed.

THE *PRN* GENE CLUSTER IN *ASPERGILLUS NIDULANS*

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One of the few examples of clustering of functionally related genes in an eukaryote is the *prn* cluster involved on L-proline catabolism in *Aspergillus nidulans* (Arst and MacDonald, *Nature, 254*, 26, 1975). Proline is converted to glutamate in two steps, catalysed respectively by the enzymes proline oxidase and pyrroline-5-carboxylate dehydrogenase, and mutations preventing proline catabolism map in four tightly linked genes, *prn*A, *prn*B, *prn*C, and *prn*D. The map order is *prn*A-*prn*D-control region-*prn*B-*prn*C. Mutations in *prn*B can lead to loss of the proline permease. *prn*D is probably the structural gene for proline oxidase. *prn*C is the structural gene for pyrroline—carboxylate dehydrogenase. Mutations in *prn*A can lead to loss of both of these enzymes and, under some conditions, to reduced permease activity. However, conditional *prn*A mutations do not seem to affect the properties of either enzyme when formed under permissive growth conditions. Therefore the *prn*A product may have a positive regulatory rather than a strucural role. The use of deletion mutations beginning in *prn*D and ending in *prn*B shows that the control region probably contains a receptor site for a positive control product necessary for full expression of *prn*C. The *prn* region is amenable to mapping using crosses with point mutations and/or deletions as flanking markers now available on either side.

FACTORS AFFECTING SPONTANEOUS MUTAGENESIS IN CONTINUOUS CULTURES OF *SCHIZOSACCHAROMYCES POMBE*

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The rate of spontaneous mutation to resistance to the 12, 13 epoxytrichothecene trichodermin has been determined under different growth-limiting conditions in continous cultures of the microbial eukaryote *Schizosaccharomyces pombe*. In agreement with data obtained in bacterial systems by previous workers, the kinetics observed for the accumulation of mutations is found to be dependent upon the nutrient used to limit the growth of the population. Under conditions of glucose-limitation mutation accumulation is proportional to the rate of cell division, while under various amino acid limiting regimes it becomes proportional to chronological time. Possible explanation for these observations will be discussed.

PHYSICAL MAPPING OF GENES AND CROSSOVER EVENTS BY ANALYSIS OF HERPES SIMPLEX VIRUS INTERTYPIC RECOMBINANTS

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The genome structures and polypeptides induced by HSV-1/HSV-2 recombinants, including those isolated by Timbury and Subak-Sharpe (*J. Gen. Virol., 18*, 347, 1973), have been analysed.

While HSV-1 and HSV-2 have a genome structure consisting of a long and short unique region, each bounded by inverted repetitions (Sheldrick and Berthelot, *Cold Spring Harb. Symp. Quant. Biol., 39*, 670, 1974) they differ considerably in their restriction endonuclease cleavage patterns. From analyses of recombinant DNAs with restriction endonucleases we can determine the positions of the crossover events that generated the recombinants, assign map positions for several temperature-sensitive mutations and, together with cross-hybridization studies, align the physical map of HSV-1 and HSV-2. In addition, differences in electrophoretic mobility of HSV-1 and HSV-2 induced polypeptides enable these products to be identified in cells infected by the recombinants. Correlating this information with the genome structures of the recombinants has enabled us to locate the genes for many polypeptides. Of particular interest are the 21,000d and 175,000d polypeptides of HSV-1 which both map in the short region even though they exhibit very different kinetics of synthesis.

MAPPING OF HERPES SIMPLEX VIRUS TYPE 1 (HSV 1) GENES BY MARKER RESCUE

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DNA extracted from wild type HSV-1 virions has previously been shown to be capable of initiating plaque formation in monolayers of susceptible cells (Sheldrick *et al.*, *PNAS*, *70*, 3621, 1973; Graham *et al.*, *Nature New Biol.*, *245*, 265, 1973). Using a modification of the calcium phosphate technique (Stow and Wilkie, *J. Gen. Virol.*, *33*, 447, 1976) it can be demonstrated that neither fragmented wild type DNA, nor DNA extracted from temperature sensitive (*ts*) mutants of HSV-1, give rise to detectable progeny following infection at the non-permissive temperature (38·5°). However mixed infection with random fragments of wild type DNA and intact *ts* DNA at 38·5° results in the appearance of many plaques due to virus replication. Progeny tests indicate that both complementation and recombination can occur.

Moreover, selected *ts* markers have been rescued using isolated restriction enzyme fragments of wild-type DNA. Two early mutants have been shown to map in the short repeat regions of the genome described by Sheldrick and Berthelot (*CSHSQB*, *39*, 667, 1974), whilst two late mutants map in the long unique region. A similar approach has enabled us to locate the virus coded thymidine kinase gene close to these late mutants. We can thus begin to correlate the physical map of HSV-1 with the previously published genetic map for the *ts* mutants (Brown, Ritchie and Subak-Sharpe, *J. Gen. Virol*, *18*, 329, 1973).

NON-PHOTOREACTIVEABLE ENDONUCLEASE V-SENSITIVE SITES INDUCED IN THE DNA OF BACTERIOPHAGE T4 BY NEAR UV (320 NM) IRRADIATION

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Most studies on the biological effects of UV have involved the use of far UV (chiefly 254 nm), but UV from 300-320 nm is much more relevant to environmental mutagenesis. The most important 254 nm-induced photoproducts, both in yield and harmful effects, are cyclobutane pyrimidine dimers. However their relative importance following 320 nm irradiation is less certain. We have previously shown that DNA from 320 nm-irradiated bacteriophage T4, but not from 254 nm-irradiated T4, contains a photoproduct which can be recognised by T4 UV endonuclease (endonuclease V) but cannot be photoreactivated (*Mutation Res.*, in press). This photoproduct is therefore not a normal cyclobutane pyrimidine dimer. These experiments have been repeated with DNA from a mutant of T4 containing cytosine in its DNA rather than hydroxymethycytosine as found in wild-type T4 DNA. In the cytosine containing T4 DNA, unlike the hydroxymethy-cytosine containing DNA, all the T4 endonuclease V-sensitive sites induced during 254 and 320 nm irradiation, can be photoreactivated. Thus the photoproduct formed in wild-type T4 is presumably a photoproduct of hydroxymethycytosine which cannot be photoreactivated and is only formed on exposure of T4 DNA to near UV.

GENE ORGANIZATION AND EXPRESSION OF PLASMIDS Co1E1 AND Co1K

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Co1E1 Co1K are both small (molecular weight $4\text{-}5 \times 10^6$) multicopy plasmids that encode the synthesis of antibiotic proteins (colicins E1 and K) that have similar biological activity, though they bind different receptors on the cell surface. We have shown that the plasmid DNA molecules show greater than 50 per cent homology, and behave similarly in their ability to replicate in the absence of protein synthesis and in their quantitative requirement

for DNA polymerase I. Heteroduplex studies show that both plasmids share sequences in the region of the origin of replication, and sequences containing parts of the colicin genes. Regions of DNA involved in conjugational mobility do not seem to be homologous though Col k can complement the transfer defect of non-transmissible Col E1 mutants.

ANALYSIS OF SPONTANEOUS LAC-PERMEASE NEGATIVE MUTANTS IN A KLEBSIELLA STRAIN CARRYING TWO LAC OPERONS

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Klebsiella V9A carries two *lac* operons, one each in the chromosome and on a plasmid (F_K*lac*). Loss of the plasmid leads to a weak Lac$^+$ phenotype (on MacConkey agar) due to the chromosomal operon. Mutations in the plasmid Lac-permease gene produce a Lac$^-$ phenotype, but such clones can revert to the weak Lac$^+$ phenotype by loss of the mutant plasmid. The mutant clones are not completely Lac$^-$, since they can grow on a high concentration of lactose as carbon source (Reeve, *Genet. Res.*, *28*, 61, 1976).

Hobson, Gho and Muller-Hill (in press) have prepared a series of overlapping deletion mutants of the K12 LacY gene, and these have enabled us to map the permease mutants of F_K*lac*, which can recombine with the K12 *lac* operon. Of five mutations tested, three map near the left end and two near the middle of the Y gene. One can revert to wild-type by a second mutation in the plasmid. The plasmid DNA can substitute for any missing part of the K12 Y gene, indicating their close homology. The significance of these results will be discussed.

ABSTRACTS OF DEMONSTRATIONS

ILLUSTRATION OF INTRASPECIFIC ANTAGONISTIC PHENOMENA IN NATURAL POPULATIONS OF WOOD-DECAYING BASIDIOMYCETES

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A demonstration of the phenomena and techniques described in the contributed paper (Todd and Rayner, this meeting) on this subject will be presented. This will include examples of stumps and logs before and after incubation, agar plate interactions and microscopic perparations illustrating interactional phenomena.

STRUCTURE OF HUMAN GENEALOGIES

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Complete genealogies of isolated small human populations exhibit many interesting features, and the addition of genetical information about living members opens the way to investigations into the likely genotypes of the founders.

Three genealogies (collected by other workers, and as yet unpublished) will be displayed in graph-theoretic form.

CHROMOSOMES OF SOME HETEROTHALLIC SPECIES OF *PHYTOPHTHORA*

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Meiosis in a number of heterothallic species of *Phytophthora* will be illustrated. They will include the " L " (large) and " S " (small) chromosome types at present attributed to *P. palmivora* (although probably different species) and tetraploid British isolates of *P. infestans*.