THE GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers presented at the HUNDRED AND SIXTY-NINTH MEETING of the Society held on Thursday and Friday, 13th and 14th July 1972, at ABERYSTWYTH in the Department of Agricultural Botany, University College of Wales, and the Welsh Plant Breeding Institute respectively.

THE RELATIONSHIP BETWEEN CANOPY STRUCTURE AND PRODUCTIVITY IN RYEGRASS (*LOLIUM* SPP.) AND ITS PLANT BREEDING IMPLICATIONS

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Studies have been carried out to examine the relationship between canopy structure and productivity in ryegrass. In particular the relationship between the individual components of canopy structure, (tiller angle, leaf size, leaf rigidity, leaf angle, tiller number) and productivity have been examined in plant material from (*a*) within a ryegrass variety and (*b*) a wider range of material resulting from a diallel cross between six ryegrass varieties of very contrasting canopy structure.

Canopy structure and its components, particularly leaf length and tiller angle, were closely related to total annual yield. Considerable variation exists within and between varieties in canopy structure and its components; furthermore all the components are highly heritable.

A programme of divergent selection is being carried out for the components of canopy structure and the sward yield of these lines is being measured. Such selection has already proved rewarding in terms of the production of material with higher productivity. For example a family selected from within *L. perenne* cv S.321, and possessing erect tillers and long rigid leaves produced 33 per cent. more dry matter than the original variety.

An encouraging feature of this work is that it has proved possible to identify characters which can be measured on young spaced plants and which are related to sward yield.

The plant breeding implications of these results are discussed.

TRISOMICS OF RYEGRASS

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Perennial ryegrass, *Lolium perenne* L. is a cross-pollinating, diploid ($2n=14$) species. Primary trisomics ($2n=15$) and double trisomics ($2n=16$) were obtained in the progeny of a hyper-triploid plant ($2n=22$). Meiotic studies showed differences in their mean chromosome association, chiasma number and univalent frequency; a parallel variation in their pollen fertility and seed set was observed. Variation in leaf and spike morphology along with that in the meiotic behaviour suggested that the extra chromosomes were different. Karyotype analysis in a few cases has confirmed the trisomy for chromosomes II, III, VI and VII. The possible use of trisomics for studies on gene location, chromosome mapping and genic-cytoplasmic interaction will be presented.

NUCLEAR DNA CONTENT AND MINIMUM GENERATION TIME

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From comparisons of widely unrelated species, nuclear DNA content is known to be positively correlated with the durations of several developmental processes including minimum cell cycle time and meiotic duration. Since nuclear DNA content apparently determines the rate of development at the cellular level, it is probable that it could influence the rate of development and amount of growth of the whole plant, and thereby determine its minimum generation time.

To test this hypothesis, minimum generation time was compared with cell cycle time in somatic tissue, meiotic duration in the anther, and nuclear DNA content for nearly 300 species. Each character showed the expected relationship to minimum generation time, *i.e.* all species with very short generation times had very short cell cycle and meiotic times, and very low nuclear DNA content, while all species with very high nuclear DNA content had long cell cycles, long meiotic divisions, and long minimum generation times. For example, in the diploid monocots, the mean nuclear DNA content was about 7 picograms (pg) for ephemeral species, 18·5 pg for annuals 16·1 pg for perennials which normally flower in their first year (facultative perennials) and 112·9 pg for perennials which do not flower until after their first year of growth (obligate perennials).

It is concluded that nuclear DNA content determines the minimum generation time. Thus, a low nuclear DNA content is an essential prerequisite for the ephemeral life habit, while the perennial life habit is obligate to all species with very high nuclear DNA content.

Nuclear DNA can affect the phenotype by its physical properties (*i.e.* its mass) as well as by its informational content—the genotype. The term " nucleotype " is used to describe nuclear characters other than the informational content of nuclear DNA which affect the phenotype.

NEW EVIDENCE ON THE GENETIC SYSTEMS CONTROLLING MEIOTIC CHROMOSOME PAIRING IN THE *TRITICINAE*

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Hybrids between wheat, *Triticum aestivum*, and either of the two outcrossing diploid relatives *Aegilops mutica* or *Aegilops speltoides*, segregate to give four classes differing in their degree of meiotic chromosome pairing, irrespective of the presence or absence of B chromosomes, indicating a four-allele two-locus system of pairing control on the A chromosomes of the *Aegilops* genome. The loci appear to have no detectable effect on pairing in the diploid populations but this could be due to a bias in sampling since a high frequency of double heterozygotes occur in these populations. Similarly no effect on pairing occurs among 49-chromosome hybrids of the first backcross generation of (*T. aestivum* × *Ae. mutica*) × *T. aestivum*. Isolation of a satellited chromosome of *Ae. mutica* probably carrying both the pairing control loci induces homoeologous pairing in a wheat background only when disomic for a critical region of the chromosome.

Triticum/Aegilops hybrids containing B chromosomes show abnormalities of meiotic and pre-meiotic spindles and B chromosomes from *Aegilops mutica* have been found to interact with specific gene loci in *Triticum* which prevent asynapsis at low temperatures. The interpretation of these results and their relevance to the evolution of the diploidising system in polyploid wheat will be discussed.

BREEDING PEAS WITHOUT LEAVES

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A series of mutations which affect leaflet and stipule formation is available in peas. The most extreme form of plant that can be produced has no leaves and only very small stipules. Reducing the amount of pea haulm in these ways might be of value in speeding up the processing of the crop and in providing some measure of resistance to attack by pathogens and insect pests.

The genetics of the various leaf forms will be discussed together with the results of some preliminary experiments to measure photosynthetic efficiency.

GENETIC CONTROL OF ENVIRONMENTALLY INDUCED CHANGES IN *LINUM*

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Varieties of flax in which heritable changes can be induced by growing the plants in different environments are called *plastic* varieties. Large differences in plant weight and in amount of nuclear DNA can be induced in them. Other varieties are *non-plastic* either because they are genetically different or because their ancestral environments have stabilised them, or for both reasons.

Crosses and backcrosses made between a plastic flax variety (Pl) and a non-plastic linseed variety (R) were tested for plasticity by determining whether changes in amount of nuclear DNA are induced in them when grown in the specific inducing environments of nitrogen and phosphorus. Pl was found to contain a nuclear factor and a cytoplasmic factor both of which must be present for the plastic character to appear. R contains neither of these factors but it has sites, in common with Pl, at which changes in amount of nuclear DNA occur when the Pl nuclear and cytoplasmic factors are introduced. These genetic elements can be formally separated into regulator and structural genes.

DEVELOPMENTAL GENETICS OF VARIATION IN FLOWERING TIME IN *ANTIRRHINUM MAJUS*

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The study of the inheritance of continuous variation is usually performed by inferences made from certain statistics such as variances and covariances, it being assumed that there is little prospect of identifying any of the individual genes responsible for the variation.

Using inbred lines of *Antirrhinum majus* we have, with reasonable certainty, identified and located a gene controlling variation in flowering time. This is a trait which shows continuous variation, but by dealing with components of development (time of bud formation) and by using specific controlled environments (25° C., 16 hr photoperiod) discontinuous segregation was detected in certain crosses. The gene responsible appeared to be linked to two flower colour marker genes. Under other environments it prodcued a diminished phenotypic effect, but there was some evidence that at a lower temperature a second locus may be responsible for most of the variation (also producing a change in the ranking of the parental lines).

The implications for the study of the developmental genetics of continuous variation will be discussed.

NUCLEAR CONTROL OF THE PATTERN OF EXTRA-NUCLEAR PLASTID INHERITANCE

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Two cultivars of zonal *Pelargonium* have been found to give quite distinct patterns of biparental plastid inheritance. Breeding experiments strongly indicate that the two patterns are controlled by alternative alleles of a nuclear gene, named Pr_1 and Pr_2, with a direct effect on plastid replication. It is further suggested that the major control of plastid inheritance is by the female parent, because the female produces the eggs, and the nuclear genotype of the eggs determines the behaviour of the plastids.

THE *LI* LOCUS OF *TRIFOLIUM REPENS*

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Cyanogenesis in *Trifolium repens* involves the release of HCN by hydrolysis of the cyanoglucosides, linamarin and lotaustralin. The enzyme, linamarase, which catalyses this reaction, has a broad substrate specificity and will hydrolyse other β-glucosides and β-galactosides. The activity of this enzyme is controlled by the *Li* locus at which two alleles, *Li* and *li*, were originally recognised. Plants carrying *Li* alleles have an active linamarase, while *lili* plants are unable to hydrolyse the cyanoglucosides, but retain low levels of activity against other subtrates. There is a dosage effect of *Li* alleles on linamarase activity with heterozygotes having intermediate activity levels.

Immunological tests have shown that *lili* plants do not contain a protein antigenically related to the normal enzyme. The residual β-glucosidase and β-galactosidase activities of *lili* plants differ from the *Li*- controlled activities in their responses to inhibition and heat-inactivation tests.

A new allele of the *Li* locus, controlling low levels of linamarase activity, has been identified.

DISEASE RESISTANCE—THE BREEDERS' DILEMMA

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The major contributions made by breeders to the improvement of cereal yields so far, have been the shortening and strengthening of the straw and modification of the pattern of fertile tiller production. Attempts to reduce losses due to diseases, in particular those caused by air-borne pathogens, have met with mixed success.

The problems of breeding for increased disease resistance will be considered as three levels of specificity. (1) " Race specific " resistance effective against pathogenic races of a single species. It is usually controlled by single dominant, incompletely dominant, or recessive major genes, and is expressed as immunity or a hypersensitive reaction. (2) " Race non-specific " resistance effective against all pathogenic races of one pathogen. The expression of this form of resistance varies, and the highest levels of resistance to mildew in oats and rhynchosporium and mildew in barley, investigated so far, are not mono-genically controlled. (3) " Generalized " resistance, effective against several pathogenic species. It will be emphasized that as the mechanisms involved in the expression of these forms of resistance are investigated in detail, this classification becomes less clearly defined.

The rate of emergence of new pathogenic variants able to overcome the type of resistance utilized by the breeder is of fundamental importance. The long-term strategy to be employed in utilizing the various forms of resistance to provide permanent protection against yield loss due to disease will be raised for discussion.

THE STUDY OF ECOLOGICALLY MARGINAL POPULATIONS

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There has been speculation but little serious work on the ecology and genetics of ecologically marginal populations. However, scattered through the literature there is quite a lot of relevant information. An attempt will be made to draw together this information and suggestions will be put forward for further study.

PROBLEMS OF CHROMOSOME MANIPULATION IN PLANT BREEDING

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The introduction of alien variation from wild species into cultivated crops and combining the desirable characters of two related crop species in a novel form can not usually be achieved by conventional plant breeding methods because of differences in cytogenetic constitution. Although many of our crop plants have evolved by the combination of genomes of different species in nature, the synthetic production of new species has presented a number of problems associated with cytogenetic stability. The success of introducing and/or combining the genome of one species with that of another depends on the flexibility of the systems controlling inter-specific chromosome pairing in species hybrids. This and other problems will be discussed in relation to the *Festuca-Lolium* complex where inter-specific chromosome pairing is high and in the *Avena* where pairing is restricted to homologous chromosomes.

CYTOGENETICS AND WHEAT BREEDING

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Cytogenetic techniques in the hexaploid wheats provide a powerful means of genetic analysis. In wheat breeding the results of these analyses have been exploited in the manipulation of the genetic control of chromosome behaviour and have led to the introduction of useful genes from the close relatives of wheat. The transfer of single chromosomes and entire genomes from related species into wheat has also been accomplished and some of these transfers have been utilised in agriculture.

The analysis of agronomic characters using cytogenetic techniques has been carried out to give detailed genetic descriptions of the differences occurring among wheat varieties. The results of these investigations provide an account of the genetic structure of wheat varietal populations and the relationship that can occur between characters in their genetic control. The ultimate aim of these studies is to present the wheat breeder with a description of the " ideal " agricultural genotype and consequently to lead to a definition of breeding objectives and selection limits.

THE USE OF CHROMOSOME FRAGMENTS IN HYBRID BARLEY PRODUCTION

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Balanced tertiary trisomics are being used in commercial production of hybrid barley. The BTT system makes use of three components: an extra chromosome,

a genetic recessive male sterile gene, and informational genes. Improvements of the BTT system are being developed. One area of improvement concerns extra chromosomes. The extra chromosome must be incapable of independent transmission; it must be accompanied in its inheritance by a complete set of normal chromosomes. Also, it must not be transmitted through the pollen but must be transmitted through the eggs. The male sterile and informational gene loci must be located on the extra chromosome. Centric chromosome fragments can serve as extra chromosomes. It is possible to select fragment trisomics that are almost as vigorous as their diploid sibs. If the fragments are a result of terminal deletions, non-homology of chromosome ends results in the fragment behaving as a univalent during meiosis. The major difficulty with using fragments as extra chromosomes is pollen transmission. The fragments that are most advantageous in BTT breeding systems are the ones most likely to be transmitted through the pollen. Pollen transmission can be prevented by inducing a mutation for pollen lethality on the fragment.

BIVALENT-FORMING NATURAL AUTOTETRAPLOIDS IN THE *BRASSICEAE*

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During a survey of the cytotaxonomy of *Brassica* and its allies 35 diploid genomes have so far been located, together with 10 natural derived tetraploids. Of particular interest are 5 of these tetraploids which are essentially bivalent forming but which yield species hybrids in which autosyndetic pairing of their chromosomes is complete. It is suggested that these tetraploids are genomically of the type $G_1G_1G_2G_2$ in which G_1 and G_2 are structurally similar but prevented from pairing with one another by a suppressor mechanism, the suppression being overridden in hybrids of the type $G_1\ G_2\ X$.

It will be argued that meiotic pairing control of this type (closely akin to and possibly essentially identical with, Riley's 5B system), based not on chromosome structure *per se* but on the physiology of meiosis, could be a force of the greatest evolutionary significance, especially when acting at the diploid level.

NEGLECTED CHROMOSOMES

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Supernumerary, B chromosomes have been found in more than 200 species of flowering plants. The number of B's per plant varies within and between populations and there is every reason to suppose that this variation is adaptive. Their effects upon plant growth and development are widespread. They affect chromosome behaviour during cell division, both at mitosis and meiosis; they influence yield and fertility. It is possible they may be of use in plant breeding.

GENETIC CONTROL OF CELL WALL BIOGENESIS IN *CHLAMYDOMONAS REINHARDI*

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79 mutants have been isolated in *C. reinhardi* which show a defect in some aspect of cell wall biogenesis. Electron microscopical and electrophoretic analyses of walls and of wall components have indicated the nature of some of the defects in the mutants. The results obtained with one particular mutant, CW18, will be considered, together with the genetical evidence which indicates the presence of more than one level of control of cell wall biogenesis.

ALLELIC VARIATION AND CELLULAR INACTIVATION IN YEAST

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Genetic analysis indicates that the members of a group of UV light sensitive mutants of the yeast *Saccharomyces cerevisiae* are alleles of a single gene designated *rad*-3 (Parry, Parry and Waters, 1972. *Mutation Research, 15,* 135-146). The individual alleles show significant variation in their response to UV irradiation, various modifying treatments of UV such as photoreactivation and liquid holding treatment, and to nitrous acid inactivation both in haploid and diploid cultures, but show a wild-type (RAD) response to alkylating agents.

In addition to their effects upon cell viability the individual alleles of *rad*-3 produce significant variation in their effect upon UV induced forward mutation of both drug resistance and nutritional markers.

TEMPERATURE SENSITIVE REPAIR OF UV LIGHT AND IONISING RADIATION DAMAGE IN YEAST

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The mechanisms of recovery of cells inactivated by UV light or ionising radiations have been studied by the use of mutants defective in these processes. However, such mutants suffer from a number of limitations and, in an attempt to overcome some of these, a new range of mutants of the yeast *Saccharomyces cerevisiae* termed *ts-rad* have been isolated. These mutants are characterised by reduced cellular recovery from inactivating treatment only at the restrictive temperature of 37°.

Mutants sensitive to both UV and gamma rays at the restrictive temperature have been isolated and genetic analysis indicates that the *ts-rad* phenotypes are under single Mendelian gene control.

The use of temperature switch experiments and various modifying treatments has enabled us to determine the time of action of some of the genes involved in cellular repair.

GENETIC BACKGROUND EFFECT ON MUTAGENESIS: THE INFLUENCE OF STREPTOMYCIN ON UV-INDUCED REVERSIONS IN *E. COLI*

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UV mutagenesis has been compared in the *E. coli* B/r *trp*$^-$ auxotrophic strain WWP-2 and in a streptomycin-resistant derivative of this same strain. Over a range of UV dosages and survival levels Trp$^+$ reversion frequencies in the *stm-r* strain are consistently below those obtained in the parental WWP-2 strain. A high proportion of the UV-induced reversions in both strains are due to ochre suppressor mutations.

The apparent antimutagenic influence of the *stm-r* marker upon the *trp*$^-$ ⟶ Trp$^+$ reversion system was investigated. In the *stm-r* strain Trp$^+$ reversions could be scored not only on a normal plating medium (minimal *plus* 1 μg L-tryptophan/ml *plus* acid hydrolysed casein) but also on this same medium supplemented additionally with streptomycin. It was found that the presence of streptomycin in the plating medium led to an increased reversion response with UV light. In the presence of streptomycin the *stm-r* strain gave approximately equal reversion frequencies to those observed normally in the parental WWP-2 strain. This effect was shown to be due to an enhancing effect of streptomycin upon the efficiency of some ochre suppressor mutations. In the absence of streptomycin a proportion of those Trp$^+$ revertants

due to ochre suppressor mutations escape detection in a *stm-r* genetic background (Apirion and Schlessinger, Ciba Symp. *Mutation as Cellular Process*, London 1969).

CHROMOSOME REPLICATION AS A BIOLOGICAL CLOCK IN THE BACTERIAL CELL CYCLE

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Variation of the intracellular concentration of thymidine triphosphate in *thy*$^-$ strains of *Escherichia coli*, which can be achieved by supplying their growth medium with different concentrations of thymine (Zaritsky and Pritchard, *J. Mol. Biol. 60*, 65, 1971; Beacham *et al.*, *J. Mol. Biol.*, *60*, 75, 1971), appears to affect the replication time of the chromosome (Pritchard and Zaritsky, *Nature*, *226*, 126, 1970).

The possible connection between the rate of chromosome replication and the rate of the processes leading to cell division was investigated by following the kinetics of cell divisions after " step-up " or " step-down " transitions in the thymine concentration in glycerol grown cultures of *E. coli* 15T$^-$ (555-7). These studies suggest that both the following conditions must be fulfilled before the cell divides: (*a*) at least *c.* 80 minutes of undisturbed metabolism after initiation of chromosome replication, and (*b*) completion of the corresponding round of replication. Thus, for instance, when the replication time of the chromosome is longer than 80 minutes the cell divides soon after completion rather than 25 minutes later, as it does in *thy*$^+$ cells with a replication time of 45 minutes.

This conclusion, derived from kinetic data, is confirmed also by measurements of average cell mass and DNA content in steady-state cultures of this strain growing exponentially in glycerol minimal medium containing different thymine concentrations.

GROWTH OF THE ENVELOPE OF ROD-SHAPED BACTERIA

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The faster rod-shaped bacterial cells grow the larger they become (Schaechter *et al.*, *J. Gen. Microbiol.*, 19: 592, 1958). Fast growing cells are both longer and wider than slowly growing ones (ibid), yet at any particular growth rate cells extend only in length (Marr *et al.*, *J. Bact.*, *91*, 2388, 1966). During a transition from one growth rate to a faster one (a " shift-up ") the cells, which normally increase only in length, must therefore increase in width. This apparent paradox provides a clue as to the mechanism of bacterial envelope growth. It suggests that the rate of extension in length responds to an enrichment in the growth medium more slowly than the rate of increase in cell volume, the additional mass synthesised being accommodated by a reduction in surface/volume ratio, *i.e.* by a physical distension in the width of the cell. (It is assumed that the density of the cytoplasm is the same at all conditions).

The size of cells of *Eschericha coli* is also affected by the replication time (C) of the chromosome. Since we can change C in thymineless mutants without affecting the growth rate (Pritchard and Zaritsky, *Nature*, *226*, 126, 1970) we are able to analyse the factors affecting well shape without introducing complications due to changes in growth rate.

Our data, together with those obtained from shift-up experiments, suggest that the rate of extension in length is proportional to the growth rate and the number of chromosome termini per cell.

8:0, 0:8, 7:1 AND 1:7 CONVERSION RATIOS IN OCTADS FROM WILD-TYPE × MUTANT CROSSES OF *ASCOBOLUS IMMERSUS*

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Aberrant segregation ratios of 6:2, 2:6, 5:3 and 3:5 were described from several organisms and have been explained in terms of hybrid-DNA formation between a pair of non-sister chromatids in a bivalent. Hybrid-DNA formation at the same site in *both pairs* of non-sister chromatids could produce 8:0, 0:8, 7:1 and 1:7 ratios (" wider ratios "), in addition to the " narrower ratios " mentioned. " Wider ratio " octads reported from *Ascobolus* and *Sordaria* by other authors were found by them to be spurious or extremely rare.

In the present *wild-type* (+) × *white* (*w*) crosses of the Pasadena strains of *Ascobolus immersus*, using mutants *w*–10, *w*–62 and *w*–78, " wider ratios " occurred regularly, mostly 8+ :0*w* and 0+ :8*w*. Germination and back-cross tests showed that nearly all 8+ :0*w* octads were genuine, with 4:4 segregation for mating-type, but many 0+ :8*w* octads arose by mutation at other *white* loci. Control experiments ruled out back-mutation and aggregation of spores from different asci as major causes of 8+ :0*w* or 7+ :1*w* octads.

When conversion frequencies were varied by using different crossing temperatures or strains differing genetically, the frequency of 8+ :0*w* octads bore a clear positive relation to overall conversion frequencies, reaching 1 per cent. under some conditions.

These findings will be discussed, especially in relation to possible interference between the two pairs of non-sister chromatids in hybrid-DNA formation.

THE EVOLUTION OF BASIDIOMYCETE SPECIES

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The homing of hyphae onto oidia can give viable or lethal reactions. Strains showing a lethal reaction cannot form dikaryons so that an objective test for a taxon above the species level is available. The evolution of basidiomycete species with special reference to heterogenic incompatibility and unilateral nuclear migration will be discussed with reference to the genera *Coprinus* and *Psathyrella*.