

GENETIC RESEARCH IN BRITAIN, 1939-1945

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(1) DEPARTMENT OF GENETICS, CAMBRIDGE
PROFESSOR R. A. FISHER

THE Department of Genetics, at Cambridge, is being organised with a view to carrying out research in the three fields of Animal, Plant and Human Genetics.

The colony of mice now run for about 20 years is being reorganised, with the establishment of 21 inbred lines each maintained segregating in five supposedly unlinked factors. Nearly all genetically useful genes can be thus maintained and their effects manifested in a constant genetic environment so that these effects may be studied and exhibited with a minimum of genetical disturbance. The system also provides a comprehensive study of linkage and valuable material for instruction in practical genetics.

Work is continuing on the tristyllic species *Lythrum salicaria*, having now adequate greenhouse and garden facilities. The inheritance of style-length has been shown to be tetrasomic, and it is an interesting question whether all characters in the species are inherited in the same way. Two recessive colour factors have so far appeared and the species appears to offer an opportunity of studying the complex problem of tetrasomic linkage.

The Department is collaborating closely with the serological research unit originally set up in the Galton Laboratory for the study of human genetics. This unit has been largely responsible for the elucidation of the complex genetic situation in the Rhesus factor and is continuing the study of this and other serological factors in Man.

Inbreeding is of great practical importance in animal and plant improvement, but its theory seems to have been quite inadequately explored. A somewhat fuller theoretical study of various aspects of this subject will soon be published.

(2) MEDICAL RESEARCH COUNCIL, EMERGENCY BLOOD TRANSFUSION SERVICE AT DEPARTMENT OF PATHOLOGY, CAMBRIDGE.
DR R. R. RACE

In 1940 the human blood groups called Rh were discovered and their importance in causing transfusion reactions and hæmolytic disease of the newborn was established. This was mainly the work of Landsteiner, Wiener and Levine in New York.

In 1942 this unit began to do routine Rh tests in these two groups of conditions. In 1943 one of us was free to carry out research into the Rh groups and this work has continued through the last three years.

We have been able to isolate seven allelomorphs of the Rh gene, six of which were isolated at about the same time independently in America. An "incomplete" non-agglutinating form of anti-Rh has been discovered, which is as dangerous in causing hæmolytic disease as is the complete agglutinin. This also was described simultaneously in America.

Early in 1944 our results were studied by Professor R. A. Fisher who proposed the theory, which has now received considerable support, that three closely linked loci each with at least two allelomorphs were responsible for the Rh groups. The theory demanded one more allelomorph and two more antibodies. We have recently discovered one of the two predicted antibodies.

(3) GALTON LABORATORY. PROFESSOR L. S. PENROSE

(1) Further data collected on the question of linkage between the A.B.O. agglutinogens and (i) phenylketonuria and (ii) red hair have

been consistent with previous findings. The correct method of treating the data is still in some doubt. There may be linkage in both cases but in (i) there is at least 25 per cent. crossing-over, though in (ii) there may only be as little as 12 per cent.

(2) Inheritance of the common types of psychoses has been studied on an extensive scale, paying special attention to the age of acute onset. In the first place, age of onset was shown to be a sex-influenced character. Secondly, correlation coefficients of age of onset in relatives suggest the genetic background of variation in this character is multifactorial and that possibly sex-linked factors play an important part, though the main genes responsible for the illnesses themselves are autosomal. Thirdly, combining these findings with the results of some mental and physical measurements indicates that variations in onset ages and types of mental illnesses may be conditioned by quantitative sex differences, so that the study of the genetics of mental illness may elucidate the inheritance of sex deviations in man.

(3) Analysis of new material and published pedigrees of diabetes mellitus show an incidence in sibships which can either be interpreted as due to partial sex linkage or modification by sex-linked genes (published jointly with E. Watson).

(4) Relatives of certain types of cases of developmental abnormalities show a higher frequency of the peculiar palmar dermatoglyphs characteristic of these cases than are shown by random population samples.

(4) UNIVERSITY COLLEGE, LONDON. PROFESSOR J. B. S. HALDANE

Drosophila. In all species examined spermatogenesis occurs in imagines. Thus it is possible to examine males cytologically after breeding from them and (*e.g.*) to detect XO males.

In several species yellow mutants have a cuticle more permeable to water than normal, and black mutants less. The effect of a number of eye colour genes on visual acuity has been measured.

Drosophila subobscura. In this European species we have about 50 mutants. It is so far unique in animals and plants in being a permanent structural heterozygote for 3 autosomes, which differ from one another by inversions. Flies homozygous for more than one inversion are sterile. The chromosome maps are at least 570 units long. At least one inversion gives negative interference, *i.e.* a crossover on one side of it increases the probability of a crossover on the other side. Primary non-disjunction is not rare, but there is no secondary non-disjunction. Gynandromorphs are rarely bilateral, usually fore-and-aft. Several peculiar genes are found, notably a crossveinless causing detached testis. White males are sterile as mating depends on vision. Normal females refuse to mate with yellow males.

Drosophila melanogaster. The cytoplasmically inherited agent causing sensitivity to carbon dioxide disappears when stocks are kept cold. It is not transferred to or from transplanted ovaries, and can thus hardly be described as a virus. Culture conditions can be arranged to make ebony either disadvantageous or advantageous in the struggle for existence.

Felis domestica. The Abyssinian gene transferred to a yellow produces a uniform yellow as predicted by Hagedoorn.

Homo sapiens. Spastic ataxia is due to several incompletely sex-linked allelomorphs. The differences in age of onset of a congenital disease have been shown to be due to modifiers in some cases, to different alleles in others. Hoogvliet's data, when combined with our own, show about 10 per cent. recombination between hæmophilia and colourblindness. But myopia with nystagmus shows over 50 per cent. recombination with colourblindness in White's pedigree. Retinoblastoma seems to be due to a dominant gene with about 90 per cent. penetrance and 90 per cent. lethality among those showing the phenotype. It appears by mutation with a frequency about 1 in 30,000 per generation.

(5) DEPARTMENT OF ZOOLOGY, OXFORD. DR E. B. FORD

(i) Dominance-modification in the moth *Abraxas grossulariata*. By means of + and - selection, it has been possible to alter the expression of the gene producing yellow (compared with normal white) pigment, until the heterozygotes overlap the normals in one line and the mutant homozygotes in the other, thus producing dominance-modification in a wild form.

(ii) Industrial melanism in the Lepidoptera. The heterozygous melanic forms are harder than the normal form both in *Boarmia repandata* and in *Biston betularia*. Also the melanic forms are more conspicuous than the normals in unpolluted country but less so in industrial conditions. These facts are in accord with the proposed interpretation of the phenomenon.

(iii) Chemistry of pigments in the Lepidoptera, both in varieties and in normal forms. A classification based upon chemistry accords with that which had been arrived at in ignorance of the nature of wing-pigments of these insects.

(iv) The spread of a gene in natural conditions in an isolated population of the moth *Panaxia dominula* during seven years. The frequency of the gene in nature has been ascertained year by year and its spread demonstrated. This has been related to the total numbers of the population, obtained by the method of marking, release and recapture. Modifications in the effect of the gene are being traced in nature. Such modifications have, at the same time, been studied in the laboratory, and it has been possible to modify considerably the effect of the gene by selection. It is hoped to study

the evolutionary situation involved by means of combined genetic and ecological methods. Part of this work is now ready for publication.

(6) DEPARTMENT OF ZOOLOGY, CAMBRIDGE
DR C. H. WADDINGTON

Nearly all the work was concerned with the action of genes in controlling developmental processes in *Drosophila melanogaster*. One small investigation which falls outside this field was a study of X-ray induced mutations in somatic cells from the recessive gene *straw-3* to its dominant wild-type allelomorph, a change which can be recognised in single cells. It was found that the mutation rate is about 0.5 per r-unit per 10^9 genes.

The developmental studies covered factors affecting the main organs of the adult. About 40 genes affecting wing development were studied, and some sixteen different morphogenetic processes, affected by these factors, were distinguished. In all these, the genetic effects were produced by modifying the reactions between masses of tissue, rather than as a direct result of gene action in a single cell. It was found that there are two particularly critical periods in development ("epigenetic crises") at which profound morphological alterations tend to be produced. The later of these occurs about sixteen hours after puparium formation, when the body of the fly contracts sharply from a highly inflated condition to its normal size. Minor abnormalities, if they interfere with the flow of body fluid within the integument, may at this time cause gross malformations in the final shape. The earlier crisis occurs in the last larval instar or just after puparium formation and is connected with the eversion of the imaginal buds. Irregularities in folding can apparently be produced by abnormal growth-rates on the tissues. The abnormal foldings lead not only to gross malformation of organs, but also to changes in the tissues or organs produced; thus wings may become converted into thoracic parts, eyes into antennæ and so on. These alterations can be produced by making up suitable combinations of genes which affect growth rate; they can also be the consequences of intense doses of X-rays during development, the primary effect in this case also being apparently exerted on the growth rate.

Studies were made (largely by Pilkington) on the genetic control of the development of the eyes. The genetic effects were shown to be produced by alterations in the rates of division of cells, in the mutual arrangement of small groups of cells, and by the degeneration of certain cells.

A number of genes influencing the bristles were also studied, in collaboration with A. D. Lees. Only two cells are normally concerned in the development of each bristle, and the gene actions affect mainly the number of divisions, the relative positions of the cells

and the rate and kind of the secretion of bristle substance. A physico-chemical study by Lees and Picken made it possible to give an account of the shape of the bristle in colloid chemical terms.

An investigation of some of the body colour genes attempted to interpret their action in terms of the tanning reaction found in the epidermis of other insects, and to elucidate the connection between the gene effects on the adult and on the puparium.

(7) INSTITUTE OF ANIMAL NUTRITION, CAMBRIDGE DR J. HAMMOND

Reciprocal crosses between the small Shetland pony and the large Shire horse showed a maternal influence on the inheritance of size (Walton and Hammond, *Proc. Roy. Soc. B.*, 125, 1938), have been followed by back crosses to the pure breeds, but insufficient numbers have yet been obtained to give conclusive results.

The finding that the amount and extent of the hair on the tail of the lamb at a month old is an indication of the quality of the wool in the adult fleece within a breed (Thomasset, *J. Agr. Sci.*, 28, 1938) was followed by a classification of the tails of many British breeds. It was found that the same relationship held as within a breed. Romney sheep are now being inbred and selected for hairy and non-hairy tails in separate inbred lines from the same stock.

Inbreeding in Large White pigs has been continued successfully and the experiment is now in the twelfth generation. The effects on the conformation and composition of the carcass of rearing these on different planes of nutrition have been reported (McMeekan, *J. Agr. Sci.*, 30 and 31, 1940 and 1941).

Different strains of rabbits, inbred for some 30 generations, have been crossed together and observations made on the inheritance of body size, mammary gland weight, fertility, etc. The crosses have been mated back to the parent strains in successive generations to determine for each of these characters how many generations are required before the "graded-up" animal is indistinguishable from the pure bred line. This problem underlies the mass improvement of commercial animals by the grading-up by superior males. This method of "grading-up" is now being adopted for dairy cattle by War Agricultural Executive Committees, while for commercial beef cattle, the first cross with a pure beef bull which has dominant colour markings (Hereford, white-face; Aberdeen-Angus, black colour) is being used.

The practical application of artificial insemination was started by the formation of the Cambridge Cattle Breeders Society in 1942. The Society is now breeding by progeny tested bulls over half the dairy cattle in the district which it covers. This has enabled the mass grading-up of small dairy herds (over half the cows are in herds of fifteen or less) to proceed on a sound basis.

In poultry, the work has been concerned with applied genetics. In 1930 Punnett and Pease made a pure breed of poultry in which the sexes could be distinguished at hatching by the patterns of the downs. The difference depends on the imperfect dominance of the Barring sex-linked gene; it is a special case of Fisher's dominance modification by a mendelian factor. Work was undertaken to widen the range of types of these new breeds of poultry and to grade them up to commercial standards (Pease).

The sex-linked Silver gene can be used in the same way as the Barring gene to give a pure breed showing a sex-distinction in the downs (Pease).

A line of white Leghorns has been established by brother-sister mating, which after 14 generations appears to breed prolifically without deterioration. Three other unrelated lines of white Leghorns have also been established, though these are not of such long standing. All these lines have been crossed *inter se* in order to determine whether good utility poultry can be bred in this way. Preliminary results are encouraging. It has also been shown that "Top-crossing"—*i.e.* inbred ♂ × commercial ♀♀—is an effective way of breeding good utility White Leghorns (Pease and Dudley).

In all these inbred lines, it has been found that for the characters measured—growth rate and egg production—there has been no greater approach to uniformity than in control outbred stock. It would seem, then, that by selecting the most vigorous birds in each generation, we have thereby selected the birds which are heterozygous for the genes concerned with the characters measured (Pease and Dudley).

The view is widely held that the prevalent mortality in commercial poultry is in some way due to breeding from "immature" birds. It was shown, however, that mortality depended not on the age of the mother, but on whether the mother lived or died during the breeding season. Evidence supported the view that non-specific mortality was due to defects in the cytoplasm of the egg (Pease).

In Dutch rabbits a case of conjoint identical twins establishes that twinning occurs in rabbits. This probably explains odd ratios that have been recorded in rabbit litters (Pease).

The poultry work has been carried out mostly at Cambridge but also in part at Reaseheath, at the National Poultry Institute, Newport, and at the Agricultural Research Council's Field Station, Compton.

(8) INSTITUTE OF ANIMAL GENETICS, EDINBURGH DR A. GREENWOOD

Cattle and Pigs. Research on these animals has fallen into two categories: (a) Direct experimental work designed to provide genetical knowledge for application to practical problems; and (b) studies on population dynamics of existing breeds, with a view to

using the theory of population genetics to guide the choice of methods of overcoming the disadvantages of the present system of breeding domestic animals.

(a) The long-term cattle breeding trial to test the theory that important genes for milk production are sex-linked has been carried on and is approaching its conclusion. Simultaneously observations have been made on the inheritance of butterfat percentage, colour and horn type, as well as studies of fertility, œstrus during pregnancy, and the relative importance of hereditary and environmental variance in milk characteristics. Pig research has been devoted to the study of inbreeding and heterosis with particular reference to mothering qualities.

(b) The existing basis for the improvement of livestock in Britain is the pedigree system. Studies of this system from the point of view of its genetical effectiveness disclose that (1) out-crossing is almost universal and associated with considerable movements of stock, especially bulls, from region to region; (2) a very high proportion of herds in all breeds comprise less than 20 breeding females; (3) very few males or females live long enough to become fully proven; (4) the majority of breeders will not breed more than two or three generations of animals before dispersing their herds; and (5) only about 5 per cent. of all cattle are pedigreed, which means that insufficient numbers exist to provide sires for the whole commercial population.

Poultry. Apart from *ad hoc* experiments carried out during the war period the long term investigation on the inheritance of characters relating to egg production has been maintained. The flock of 500 Brown Leghorn females has been derived from a very few foundation birds to which no new blood has been introduced since 1931. Studies completed during the period under review concern: the problem of the Moulting in the Castrated Fowl; the Behaviour of Persistency (in egg production) in Individual Hens; Henny-feathering in Brown Leghorn Males; Effects of Thyroid and Gonadotrophic Preparations, and other studies on hormone action, Genetic Basis of Tumour Immunity in Fowls, and associated researches on tumour virus; The Genetics of Sexual Maturity in Hens and Fertility of Eggs.

Drosophila. A series of chemical substances has been tested for their ability to produce mutations. One group of substances was found to be as effective as X-rays, producing mutation rates up to 25 or 30 per cent. in sperm of *Drosophila melanogaster*. They further resemble X-rays in producing chromosome breaks and re-arrangements; for the doses used, however, the ratio between frequency of translocations and frequency of sex-linked lethals was significantly smaller than after irradiation with X-rays. A high percentage of mosaics in the progeny of treated ♂♂, including many gonadic mosaics for sex-linked lethals, and a significantly increased incidence of lethals in F₃, suggest that chemical treatment may produce after-

effects on exposed chromosomes. Chemicals of lesser mutagenic efficiency include one naturally occurring substance: mustard oil (allylisothiocyanate). Experiments are also being carried out with a new carcinogen, acetyl-amino-fluorene.

Genetical analysis of chemically produced "somatic mutations" in flies from treated embryos has confirmed Muller's suggestion that all, or at least most, apparent somatic deficiencies are in reality results of somatic crossing-over.

Another line of investigation is the determination of the genetic basis of specific differentiation. Studies on *D. pseudo-obscura/persimilis* hybrids have revealed hidden divergences within species connected with the presence of major mutant genes. This problem is being further investigated.

The hybrids between *Drosophila melanogaster* and *simulans* are completely sterile; gametogenesis does not even start. By crossing multiple recessive *melanogaster* triploid females with heavily irradiated *simulans* males this sterility has been circumvented and individuals have been obtained carrying chromosome recombinations like those which would result from a backcross. A genetic analysis has thus been possible of the sterility, inviability and morphologic disturbances in the hybrids. The *simulans* Y and IV chromosome have been introduced in otherwise *melanogaster* genotypes. All the analysed effects result from pairs or triplets of complementary groups of genes. In the course of this work, a study of the mechanism of dominant lethality (based on comparison between rod-, V- and ring-shaped X-chromosomes) has suggested that a single-hit effect, presumably single breaks followed by sister reunion and loss of the chromosome, is the main cause of dominant lethality (Muller and Pontecorvo).

Mammalian Sex-chromosomes. The sex-chromosomes of mammals are generally heterochromatic. It is very notable that in the X-chromosome the pairing and the differential segments, though both heterochromatic, show in many species a distinct heterochromatic cycle. This fact, together with the rarity of sex-linked genes in mammals and the many other properties of heterochromatin, has led to the suggestion that a heterochromatic block may be the visible result of repeated replicas of the same gene, or group of genes, lying close together on the chromosome (Pontecorvo). Nucleic acid starvation is responsible for non-spiralisation of heterochromatin in the hamster (Koller).

Heterokaryosis in Microorganisms with Multinucleate Cells. The nuclei of a cell may be genetically different either as a consequence of mutation or as a consequence of exchange of nuclei with other cells. Segregation of the different kinds of nuclei may follow from a random assortment at cell division. A mechanism of this sort may substitute the familiar one of alternation of karyogamy and meiosis, and, in fact, it is enormously widespread, sometimes side by side with the latter, in many groups of microorganisms. In a growing

colony the fittest proportion of nuclei of different kinds is kept by selection. Varying the external conditions immediately alters this proportion. "Balanced" heterokaryons have been obtained in filamentous Fungi (*Penicillium notatum*, *Aspergillus oryzae*).

(9) BOTANY SCHOOL, CAMBRIDGE. DR D. G. CATCHESIDE

Most work has been done on the effect of ionizing radiations on chromosomes, especially with a view to an analysis of the mechanism of breakage and reunion. D. E. Lea (Strangeways Laboratory) has collaborated in this work, in which J. M. Thoday, J. P. Kotval and L. H. Gray (Mount Vernon Hospital) have played a part. Studies have been made on the effects on the chromosomes of *Tradescantia* at the first and second microspore divisions of (a) different doses and intensities of X-rays and γ -rays at various temperatures, (b) different wavelengths of X-rays, (c) neutrons and α -rays. The main results are as follows: Neutrons are more efficient than X-rays in producing breaks (10). Two-break aberrations, e.g. interchanges, are proportional to the first power of the dose in the case of neutrons but to the square of the dose in the case of X-rays and γ -rays. Interchanges produced by X-rays are therefore mainly due to two separate hits by ionizing particles, while those produced by neutrons are mainly one hit. The neutron work enables one to show that a fairly considerable number of ionizations spread across the chromosome are needed to break it; and that X-ray breakage is mainly due to the densely ionized tail of the electron track. This agrees with the finding that some soft X-rays are more efficient than medium and hard ones, there being an optimum of about 4A.

About 90 per cent. of the chromatid breaks primarily produced by X-rays undergo restitution, their life as free breaks averaging about four minutes at 20° C. The distance apart at the time of production of breaks that take part in the interchanges is of the order of 1 micron or less.

A second group of studies has dealt with X-ray breakage in *Drosophila melanogaster* in relation to dominant and recessive lethals. A consistent interpretation of lethals is obtained by regarding them as chromosome aberrations of various kinds, whence an estimate of the breakage frequency may be derived. This estimate agrees well with one independently derived from a comparison of sex ratio distortion and chromosome structural change in ring-X and rod-X stocks. A consideration of the evidence suggests that the radiation data give the best available estimate of the size of the gene, probably correct to a factor of two in diameter.

H. L. K. Whitehouse has studied the analysis of tetrad segregation in *Neurospora* and produced a map of the sex chromosome of *N. sitophila*. Catcheside has shown that Zickler's data on *Bombardia lunata* demonstrate polarised segregation of a gene to one end of the ascus

rather than the other. J. B. S. Haldane (University College, London) and Whitehouse have found an excess of asymmetrical post-reductions in asci of *Neurospora sitophila*.

In *Oenothera*, the position effect found by Catcheside gives variegation of the allelomorphs P^r and P^s and also of S which is about 8 units from the P locus. The behaviour is complicated in some stocks by the presence of a tandem duplication of the P-S region. The duplication and a corresponding deficiency arise spontaneously presumably by unequal crossing-over. Structural analysis of some complexes has been completed.

J. L. Crosby has studied the distribution in nature of the long homostyle type of *Primula vulgaris*. In two areas the self fertile long homostyle has largely replaced the self sterile, interfertile pin and thrum types. The viabilities of homozygous and heterozygous long homostyles are under investigation.

(10) THE STRANGWAYS LABORATORY, CAMBRIDGE

DR D. E. LEA

Comparison of the efficiencies of X-rays, neutrons and alpha-rays in inducing lethal mutations can be used to estimate the number of genes in *Drosophila*. The same method can be applied to viruses and bacteria if one makes the assumption (for which there is some evidence) that their killing is analogous to lethal mutation. The results obtained are, that a small bacteriophage (S-13) and the crystallizable plant viruses are single naked genes (confirming a speculation of Muller, 1922); that larger phages (C-36 and Staph-K) contain several genes; that a large animal virus (Vaccinia) contains several hundred genes and is to be regarded as a single-celled organism; and that *Bacterium coli* contains about a thousand genes.

Observations on Feulgen-positive, chromosome-like bodies in bacteria, first described by Stille, 1937; Piekarski, 1937-1940; and Neumann, 1941, have been reinvestigated and confirmed by C. Robinow for many different species. In some species such as *Pseudomonas begoniae* and *Ps. malvacearum* the nuclear structures can be demonstrated by ordinary methods, but usually it was found necessary to aid the differentiation of chromatin and cytoplasm by a pre-treatment with warm hydrochloric acid (Piekarski, 1937).

(11) JOHN INNES HORTICULTURAL INSTITUTION

Cytology. Dr C. D. Darlington

New descriptive work on chromosomes has been concerned with the study of the centromere (the gene of movement), the origin of iso-chromosomes with identical arms, and the behaviour and genetic value of supernumerary chromosomes such as exist in equilibrium in many species of plants and animals although mechanically disfavoured. Experimental work has consisted in the study of the effects

of temperature, drugs, nutrition and disease in upsetting the spindle, in breaking the chromosomes, and in changing the cycle of nucleic acid formation and attachment (Barber, Callan and Koller).

Observations of La Cour on these lines have helped in understanding the development of the blood in mammals. Diseased conditions of the blood, such as pernicious anæmia in man, have shown abnormal production and distribution of nucleic acid as between cells of opposite types (red and white) and consequently as between their chromosomes. In this situation and in its consequences there is an analogy with the new observations on Cancer by Koller. These enquiries have laid the foundation of a new approach to the study of the breakage of chromosomes by X-rays. They have made it possible to use X-ray breakage as a means of studying many general properties of the physiology of the nucleus. The general conclusion is that the breakability and rejoinability of chromosomes depend on their nucleic acid charge (Darlington and La Cour).

New reference books have been published on cytological technique and the chromosome numbers of plants.

Genetics. Dr K. Mather

The properties and organisation of the polygenic systems, concerned in the inheritance of continuously varying quantitative characters, have been investigated in a number of plants as well as in *Drosophila*. Change of a character under selection has been related to the balance of polygenic combinations (which are carried, at least in part, by the heterochromatin), the destruction of this balance by recombination, and the correlated responses in other characters where the controlling genes are intermingled along the chromosomes. Polygenic balance is produced and maintained by natural selection, and decays when selection ceases to operate. Thus balance is related to the breeding system, for this determines whether homozygotes or heterozygotes shall be exposed to selective action. The breakdown of breeding systems by hybridisation and selection has shown that they themselves depend for their existence on polygenic adjustment, though their immediate operation may depend on major genic differences. Isolation in plants and animals sometimes depends on the same basic mechanisms which determine the breeding systems within species. Methods have been developed for the analysis of polygenic variation into its components, for the purpose of predicting selective advances.

The relation of the isolation requirements or crop plants in seed production to breeding systems and bee behaviour has been investigated, and improvement work has been carried out with tomatoes, sweet corn, beans and drug plants.

Pomology. Mr M. B. Crane

Work on the improvement of crop plants has been carried out, especially with cherries, plums, apples, pears, tomatoes, blackberries

and raspberries. Tomatoes have shown useful heterosis. The advantages of sexual reproduction in raspberries, to replace vegetative reproduction, are being investigated. The problem of rogues in tomatoes and in potatoes has been attacked.

Incompatibility in autotetraploid plants has revealed a complex interaction of different S alleles in diploid pollen-grains resulting in a suppression of the effect of the S genes in producing incompatibility. This suppressed action has been used as a selective method to produce triploid forms of apples and pears.

The natural mutation rate of S alleles has been determined in *Prunus* and *Oenothera*. On this theoretical basis a method of producing self-fertile varieties of fruit trees has been developed.

Studies on the action of various chemicals on mitosis has led to (1) a better understanding of abnormal growth, as in malignant tumours and (2) a more effective control of mitosis making the induction of polyploidy more easy in such woody and relatively slow growing plants as apples and pears. Polyploids of these fruits have now been produced.

Work with plants with excess or deficiency of heterochromatin has established the role of this part of the chromosomes in regulating cell division. Moreover, the affinity between heterochromatic regions, homologous or non-homologous is responsible for secondary association of bivalents at meiosis.

(12) PLANT BREEDING INSTITUTE, CAMBRIDGE DR H. HUNTER

The war years have been devoted to breeding work in wheat, barley, oats, potatoes, peas and sugar-beet, and, in addition, to practical problems in connection with the improvement of field beans, lucerne, sainfoin, maize and certain grasses. Genetic and cytological investigations have been restricted to certain problems arising from the breeding work for the most part, but certain other plants such as flax and watercress have also been studied.

Genetics and Cytology. "Bolter" plants have been found to be genetically distinct from normal plants in one variety of potatoes, and the two types of tuber pigmentation are inherited independently. Certain species of *Solanum* are self-incompatible under Cambridge conditions (Carson and Howard).

The inheritance of certain quantitative characters, and some anomalous forms of inheritance have been investigated in oats (Carson), and the cytology of F₁ hybrids between certain spring and winter varieties has revealed cytological peculiarities (Carson and Howard).

The date of ear emergence in barley has been investigated physiologically and genetically in a number of crosses, and an explanation of progeny behaviour has been put forward (Bell). The inheritance of rachilla length has been found to depend on a system of multiple factors of an additive nature (Bell and Carson).

The amphidiploid *Brassica chinensis-carinata* has been found to behave as a tetraploid ; a new wild species of watercress is an allo-tetraploid ; and autotetraploid flax is not amenable to improvement in fertility by selection (Howard).

Breeding. Wheat breeding has been concerned primarily with the improvement of winter and spring varieties for general cultivation. The new winter variety Steadfast was released in 1939. The economic possibilities and best methods of handling interspecies crosses in wheat have been investigated (Sir Frank Engledow).

Oat breeding has included the improvement of both spring and winter types. A new winter-hardy hybrid was released in 1940 (Hunter) and is named Picton. The improvement of spring oats is being sought by attention to such characters as grain quality, yield, resistance to lodging and frit-fly resistance (Carson).

Barley breeding has resulted in the production of three new hybrids during the war. A strong-strawed spring barley for high farming conditions named Camton was released in 1939 (Hunter). The first winter-hardy two-row malting barley was put on the market in 1943 under the name of Pioneer (Bell), and a winter-hardy six-row hybrid named Prefect was released in 1944 (Bell).

The improvement of field peas has been concerned primarily with obtaining high yielding early forms (Bell). By hybridising standard English *P. arvense* forms with multipodded *P. sativum* forms and early forms from Tasmania and Tibet, improved forms have been obtained.

Methods of selection by utilising physiological characters and mature plant seeding characters have been investigated in sugar-beet breeding. *Beta maritima* is being studied with the object of including this species in the breeding programme (Bauer and Bell).

Potato breeding has been directed towards obtaining resistance to *Phytophthora infestans* and viruses. Interspecies crosses accompanied by successive back-crossing is employed, and promising results have been obtained in building up resistance to three biotypes of *Phytophthora* (Carson, Dickinson and Howard).

(13) SCHOOL OF AGRICULTURE, CAMBRIDGE SIR FRANK ENGLEDOW

The potato research scheme of the Imperial Agricultural Bureaux is the first of its kind in world-wide crop improvement, in which the various Empire countries have co-operated in sending an expedition to Central and South America, the original home of the potato, to collect as large a range as possible of the indigenous potato varieties and in testing them at Cambridge for characters useful for plant breeders. Characters such as blight resistance, virus resistance, eelworm resistance, frost tolerance, high food value and heat resistance are being studied, and already blight resistant and frost tolerant

varieties have been selected. The aim is to select out promising varieties and to effect various combinations of characters within the varieties by hybridization, so that no matter what demands are made for material by the contributing countries it would be possible to supply the right parental combination.

(14) SCOTTISH SOCIETY FOR RESEARCH IN PLANT BREEDING,
CORSTORPHINE. MR W. ROBB

Cereals. The oat is the chief cereal plant on which breeding experiments are in progress. The main objectives are to produce new varieties having a greater degree of resistance to lodging, maturing earlier and adapted to upland conditions in Scotland, and having considerable resistance to prompt germination at harvest time.

Potatoes. Throughout the war period, potato breeding has had the object of producing improved varieties suitable for cultivation in Scotland, and resistant to diseases, particularly blight and the viruses X, A, Y and leaf-roll. Potato species indigenous to Central and South America have been employed as parents along with certain cultivated varieties from Europe and the U.S.A.

Three different strains of blight have been isolated and used for test purposes. Immunity was found to be inherited in Mendelian fashion. Many seedlings, immune from all three strains, have been bred and are now undergoing trial. Blight resistance has been successfully combined with hypersensitiveness to, and hence field immunity from, viruses X and A.

Potatoes (Virus Diseases). Inheritance studies have shown that hypersensitiveness to viruses causing mosaic diseases of the potato is inherited as a dominant character showing tetrasomic segregations. The genes Na, for Virus A, Nx, for several strains of virus X, Nb for the B strain of virus X, and Nc for the two strains of virus Y, have been postulated as the determinants of hypersensitiveness. The relationships of these genes are now being investigated. A positive resistance affecting the rate of infection with the leaf-roll virus, though heritable, shows no clearly recognisable segregations and is being investigated from the aspect of polygenic control.

Grassland Investigations and Experimental Taxonomy. The scope of the above studies has of necessity been severely curtailed during the war years, although the spatial distribution of hereditary variation in ecospecific populations has received some sporadic attention. The study of populations, and in particular intra-clinal population differentiation, will be continued as soon as facilities permit. Also the breeding of specialised races of *Lolium perenne* and *Dactylis glomerata* and the fitting of these into appropriate agricultural environments.

Swedes and other Brassicas. With Swedes breeding for resistance to the diseases Finger-and-Toe and Dry-Rot, for winter-hardiness and for higher dry-matter content are the main objectives. With

Broccoli attempts are being made to breed improved winter-hardy types which are adapted to Scottish conditions.

(15) THE WELSH PLANT BREEDING STATION PROFESSOR T. J. JENKIN

The primary function of the Welsh Plant Breeding Station has been considered to be (1) to produce improved varieties and strains of crop plants (including herbage plants) and (2) to make these varieties and strains an effective factor in practical agriculture.

Herbage Grasses. In the pre-war period formal genetical studies on the herbage grasses were mainly concerned with the inheritance of seedling and other characters in *Lolium perenne*, *Holcus lanatus*, etc. The work on *Lolium* was continued during the war on a greatly reduced scale.

Prior to the war, much attention had been given to interspecific and intergeneric crosses in the herbage grasses, particularly in the two genera *Lolium* and *Festuca*. During the war years some valuable material has been lost, but many of the original artificially produced hybrids and their derivatives are still available. This work will be resumed.

One of the practical problems with which herbage grass breeders have to contend is caused by the fact that most of the species studied are normally cross-fertilised and that the available plant material is highly heterozygous while the range of plant phenotypes within a species is very wide yet finely graduated. In addition, morphological characters that can be easily observed and evaluated are exceedingly few.

In the production of an improved "strain" it has not therefore been found practicable to isolate "pure lines" in a strict sense, but it is important that, provided no contamination from outside occurs, a "strain" should be capable of maintaining its most important agricultural characteristics indefinitely when reproduced through seeds. Volunteer plants of the same species may appear in a seed crop and thus contaminate the "strain" both directly through the mechanical mixture of the seed and indirectly through cross-pollination between the strain plants and the volunteers. Moreover, a seed crop is liable to be contaminated by pollen from fields surrounding the seed production area, thus leading to appreciable departure from the intended type in the succeeding generations. In many cases the actual source of contamination leading to departure from type is not easily ascertained, and the farmer-seed-grower is inclined to put the blame on the stock seed supplied. A strain must not within itself carry genes which may combine to produce the undesired types.

An experiment was therefore planned before the war to ascertain whether the basic plant material of the S.23 *Lolium perenne* strain does carry genes that can produce off-types. A number of S.23 basic

plants have been hand-crossed, and selection has been exercised in successive generations towards the off-type. The experiment is not yet complete, but it is already clear that by selection a definite "shift" can be effected, but there is reason to believe that this "shift" has definite limits well within the range of variation in the species as a whole, so that from these particular "basic" plants the "off-types" met with during the multiplication cannot originate within the strain itself.

This particular strain also possesses another characteristic that is of great importance in relation to the value of the strain. This characteristic is easily seen but exceedingly difficult to define, and, taking the species as a whole with a wide range of variation and fine gradations, only relative observations can be made. It would seem that here also several if not very many genetic factors are involved.

It is then interesting to note that whereas in respect of the first characteristic, a definite though limited "shift" can be effected by selection, this is not accompanied by an equivalent "shift" in the second characteristic. In itself the first is of little if any agricultural importance, while the second is agriculturally very important. Thus it seems probable that the strain can be stabilised at the extreme limit of its "shift" with regard to one characteristic without materially affecting the other and more important.

Herbage Leguminous Plants. The pre-war work of the late R. D. Williams on *Trifolium* species is well known, particularly his work on the genetics of sterility in *Trifolium pratense*. At the International Genetical Congress at Edinburgh in 1939 he briefly described some of his later results, but he was not destined to carry this work farther. Fortunately, the data upon which that account was based are available, and it is expected that shortly his successor in the Clover Breeding Department will be able to publish the results in full.

Oats. Prior to the war, E. T. Jones pursued the study of "fatuoids" in oats, and certain aspects of this work were still under investigation when war intervened. In this he had been joined by W. Ellison of the Department of Agricultural Botany who studied the cytological aspects of the problem. A fair amount of work had also been done on the correlation between several pairs of characters in oats.