

BRITISH ASSOCIATION, 1948

SYMPOSIA ON GENETICS

SECTIONS D, H AND I HUMAN BLOOD-GROUPS

ABSTRACTS of Papers read on MONDAY, 13th SEPTEMBER

BLOOD-GROUPS AND HUMAN GENETICS

J. A. FRASER ROBERTS

Apart from the blood-groups there are exceedingly few common, simply inherited human traits. Thanks to the fact that dominance is often absent, or at least incomplete, the elucidation of the genetics of the blood-groups has followed closely on advances in serology ; while their great practical importance has led to the testing of millions of donors, thus permitting applications to geographical and racial variations without parallel in other living forms. A knowledge of the simple elements of genetics, together with an appreciation of the importance of multiple alleles and of Fisher's hypothesis of closely linked (or compound) genes, makes it a relatively simple matter for those who are not themselves serologists to follow these important recent advances in genetics and anthropology.

THE MULTIPLICITY OF BLOOD-GROUPS IN MAN

R. R. RACE

Blood-groups are not yet as individual as finger prints, but their inheritance is known much more precisely. There are seven firmly established systems of groups, called ABO, MNS, P, Rh, Lutheran, Lewis and Kell. The groups are determined by antigens on the red blood cells ; and an antigen is recognised when the cells carrying it are clumped, or agglutinated, by a serum containing the corresponding antibody.

The presence of an antigen is under very rigid genetic control. As far as is known the genes for each of the groups are carried on separate chromosomes, though loose linkage may yet be demonstrated between some of them.

In England the seven groups make over 20,000 recognisably different combinations ; these vary greatly in frequency. The commonest combination has a frequency of 2 per cent., while the calculated frequency of the rarest is so low that it may never have formed the blood of an Englishman.

BLOOD AND SPEECH

C. D. DARLINGTON

It has long been obvious that the enduring processes of differentiation in the use of sounds by spoken languages depended on the genetic differences of the races speaking them. Critical evidence however had to wait for the gene mapping of

large populations. This became possible with the development of blood-group surveys. A contour map of Europe for the O blood-group shows a significant relation with the history of human migrations during the last 3000 years. It also shows a significant agreement with the present distribution of the TH sound in European languages and its historic changes. It is now therefore possible to undertake the study of the relations of race and language on rigorous genetic foundations with consequences equally remarkable for the study of evolution in man and in the language he speaks.

THE ETHNOLOGICAL DISTRIBUTION OF THE Rh AND MN BLOOD-GROUPS

A. E. MOURANT

Whereas the frequencies of the ABO blood-groups show significant variations over distances of the order of 100 km., the MN and Rh groups, though less is known of their distribution, appear to vary much more gradually.

The MN groups show an almost constant frequency all over the world with certain exceptions. M is more than normally frequent among the Asiatic Indians, and among the North American Indians and Eskimos and, to a less marked extent, among the Baltic peoples. N is abnormally frequent among the Ainu of Japan, the Papuans and the Australians. MN distributions have, up to now, thrown little light on racial relationships. The Rh system gives promise of throwing much light on such connections.

In Asiatics, American Indians and peoples of the Pacific the CDe (R_1) and cDE (R_2) gene combinations predominate in varying proportions. Among Negroes cDe (R_0) is by far the commonest combination and shows that the Negroes are quite different from all the so-called Negroids of the east so far tested.

In Europe CDe and cDE are common, together with cde (r). Rh— negative people (cde/cde) amount to about 16 per cent. throughout most of Europe. Since there is a selective elimination of heterozygous Dd babies of dd mothers as a result of hæmolytic disease of the newborn, the present Rh frequencies in Europe appear to be unstable if considered over a long period. It is probable that the present distribution is due to a mixing, at the end of the palæolithic period, of a stock akin to the modern Basques, who have nearly 30 per cent. of dd (mostly cde/cde) individuals, with a predominantly Rh positive (or D) stock from the east.

HÆMOLYTIC DISEASE OF THE NEWBORN

P. L. MOLLISON

Hæmolytic disease of the newborn is a comparatively common condition, affecting about 0.5 per cent. of all infants born in this country. The very special interest of this disease lies in the fact that it has been shown to be due to a particular blood group difference between the parents. In brief, the mechanism is this: the father hands on to the foetus an antigen, Rh, which is foreign to the mother; the mother forms antibodies against this antigen and these enter the foetal circulation during pregnancy and cause destruction of the foetal erythrocytes. If the infant is born alive, the hæmolytic process comes to an end as the infant is cut off from the supply of destructive antibodies. The disease in man is paralleled by a similar condition in newborn mules. In this case the mule inherits from its sire, the donkey, an antigen which is foreign to the mare. The mare forms antibodies which in turn cause destruction of the mule's erythrocytes.

The serological basis of the disease in man has only been understood since 1941. This knowledge has proved invaluable in understanding the disease and managing it.

For instance, the occurrence of the disease can be predicted by routine testing of pregnant women for the presence of Rh antibodies and this has, in fact, become a standard practise in many hospitals. Again, Rh negative blood can be selected for the transfusion of the infant with results greatly superior to those of transfusing unselected blood.

These two pieces of knowledge are combined in the most recent treatment of this condition. Labour is induced prematurely to diminish the period for which the foetus is exposed to Rh antibodies and a massive exchange transfusion is then carried out, some 90 per cent. of the infant's own blood being progressively removed and replaced by Rh negative blood.

SECTIONS M, D AND K

INBREEDING AND HYBRID VIGOUR IN LIVESTOCK AND CROP IMPROVEMENT

ABSTRACTS of Papers read on FRIDAY, 10th SEPTEMBER

THEORY OF INBREEDING

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From the point of view of pure genetics inbreeding should be regarded as a means of manipulating the germ plasm so as to control its structure and composition, particularly in respect to the numerous invisible factors which cannot be recognised individually. In practical plant improvement this tool has proved to be enormously successful, and its success makes it certain that it will be extensively used both in animal and plant improvement in the future. A theoretical understanding of its *modus operandi* seems, however, to be lacking, and even in the field of maize genetics, where the greatest amount of work has been done, very diverse opinions are held as to the reason for its success.

Elementary considerations show that the manifest effect of inbreeding must be due to dominance, and the genetical theory of the origin of dominance throws some light on the phenomena observed in inbreeding. Selection is exercised in three distinguishable phases of the process of producing desirable hybrids. The relative importance of selection at these stages is, however, obscure and disputed. It is submitted on quantitative grounds that the essential advantage of an inbreeding programme consists in the production in great variety of material which is reliable in its breeding properties, and that it is the facility offered for increasingly accurate selection by this reliability that constitutes the essential advantage conferred by inbreeding. In the work of maize improvement a very important contribution to the accuracy of selection at this stage has been the rapid improvement in the accuracy of varietal trials supplied by replicated randomised experimentation.

HYBRID CORN (MAIZE) IN THEORY AND PRACTICE

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Corn (*Zea mays* L.) is grown in many parts of the world for animal and human consumption. Between 1930 and 1947 there has been a change over from corn varieties to hybrids in the mid-western States of America.

The species is naturally cross-pollinated by wind and genetically plants in a variety are heterozygous. Ordinary selection methods for improving varieties, *e.g.* increasing yields, do not lead to improvements. Other breeding techniques are therefore necessary.

Inbreeding corn produces a great variety of offspring. Continued selection and inbreeding produces inbred lines showing inbreeding depression but reasonably uniform and having satisfactory plant characters. Inbred strains hybridised together produce offspring showing increased vigour, such hybrids often surpassing both parental varieties in yielding capacity. Each plant is a potential yielder and the hybrid generation is uniform in appearance and in maturity.

Greater hybrid vigour results using inbreds of diverse parentage and different inbreds have different abilities to combine well with others. This is a genetical property which can be bred for.

The theories of hybrid vigour are outlined.

The various methods of inbreeding and hybridisation in commercial use are described for sweet corn (crossing two inbreds) and field corn (crossing two different F_1 's). Methods recently introduced here are given and the future of hybrid corn in this country and in the Commonwealth discussed. The co-operation of the seed trade is stressed.

CROSSBREEDING AND INBREEDING IN LIVESTOCK PRODUCTION

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There are four ways of attempting to get better performance by breeding, and the manipulation of breeding systems is one of them. It is convenient to regard inbreeding and crossbreeding as opposite deviations from outbreeding. This has the drawback, however, that outbreeding has not, in practice, the precise meaning of random matings in a closed population, but can, and does, include at times considerable elements of both types of deviation from it.

Crossbreeding has several distinct functions arising out of its genetical consequences which are (a) the production of a comparatively uniform and intermediate F_1 ; (b) a subsequent increase of genetic variation; and (c) heterosis.

Examples of (a) and (b) are:—The stratification of sheep; the importation of Canadian Tamworths and Friesians; the use of the zebu in beef cattle country of Queensland; the use of Cheviot crosses in deteriorating New Zealand pastures; and the creation of new breeds. Theoretically, heterosis should enter into these examples, and probably it does, but it is difficult to prove.

Inbreeding leads to (i) an increase of homozygosity; and (ii) the canalisation of genetic variability into differences between lines instead of among individuals. Inbreeding, even at modest rates, outstrips selection and livestock deteriorate. Subsequent crossing of lines may recover lost vigour. Occasionally, the performance of foundation animals may be exceeded.

Considerations of time and numbers make inbreeding an unsuitable technique for most pedigree breeders. The trend is to leave the risks and rewards to institutions, *e.g.* the Regional Swine Breeding Laboratory and the Hy-line chicks in the U.S.A. Organised crossbreeding works because it fulfils well-understood functions and is carried out on a breed and area basis. Inbreeding as yet has only vague intentions and depends too much on the individual animal, herd and man. The more a breeder deviates towards inbreeding, the more likely he is to end by deviating towards crossbreeding.

INBREEDING AND HYBRID VIGOUR IN THE IMPROVEMENT OF SWEDISH SUGAR BEET

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Hilleshög

The effects of inbreeding in sugar beet are : genical homogenisation (showing especially in leaf morphology) and depression of productivity and adaptability to varying external conditions, whereas chemical constitution of the root (content of sugar, K+Na, N) is not perceptibly influenced by inbreeding in itself. Size characters do not show decrease in phenotypical variation, probably because their lower vitality makes them react more to the variation in external conditions. For producing types with specific characters to which yield and vitality are not important, inbreeding is the most effective means. Inbreeding may also be of use in breaking up positive correlations between desirable and undesirable characters caused by linkage.

Selving in the author's material has not given rise to any practically useful types. Breeding by repeated selection of mother-plant families has produced some practically valuable families. Rigorous mass-selection under specified growing conditions shows some of the traits of inbreeding, *i.e.* a marked degree of genical homogenisation and stability together with decrease in adaptability. If rigorous mass selection is combined with reproduction from few parent plants even a decrease in vitality and yield may occur.

Crossing genically different types nearly always gives an increase in yield and adaptability above the parental average, and hybrids between parents not too much differing in yield mostly surpass the better parent. The use of parents of genealogically different origin usually further improves yield but this effect may simply be the result of the difference in origin resulting in greater difference between the gene complements.

Hybridisation seems to have a very slight effect upon content of sugar (decreasing), K+Na (increasing) and N (decreasing) as compared with the parental average. Hybrids between family selected strains usually do not produce as high a yield as hybrids between comparable strains genically differentiated by mass-selection under different growing conditions.

The triploids may be considered as a special case of heterozygosity. They surpass the diploids by 4-5 per cent. in yield, and the diploids in their turn surpass the tetraploids by 5-10 per cent.

GENETICAL CONSIDERATIONS IN THE UTILISATION OF HYBRID VIGOUR

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The method of inbreeding and subsequent crossing of the inbred lines is used in naturally crossbreeding species, where homozygous lines, though of course uniform, are uniformly poor. The aim of the method is to produce heterozygotes uniformly approaching the best individuals possible in open-bred varieties, and so, as groups, exceeding those varieties ; and to produce such desirable heterozygotes predictably, generation after generation.

Five problems are raised by this method of breeding :—

1. A great multiplicity of inbred lines can be raised. These must all be tested and rapid methods of sorting them out are needed. The value of an inbred line in crosses is not predictable from its own production. Combining ability is the critical character which must be measured and made the object of selection.

2. The inbreds are themselves very poor, expensive to keep and give low yields of hybrid offspring in immediate crosses. Double crossing, top crossing, and convergent improvement are all methods aiming in various ways at overcoming this difficulty.

3. The deliberate raising of hybrids demands means of making controlled crosses on a large scale. In animals and maize this is easy ; but plants with hermaphrodite flowers demand special methods. Bulk crossing in sugar beet, and the use of cytoplasmic male sterility in onions have been developed for this purpose.

4. The very uniformity of the inbreds and hybrids carries with it certain dangers. That of the inbreds leads to risk of loss of valuable genetic variation, such as is automatically maintained in the reservoir of variability of the open-bred varieties. Collections of these varieties may therefore be necessary to provide sources of future breeding material.

In the hybrids, uniformity leads to the risk of serious loss of crops through the temporary supervention of adverse conditions whose effects would be less serious on a more variable stand. Double crossing goes some way to overcome this risk.

5. The method of inbreeding and crossbreeding must inevitably be more costly than more conventional techniques of breeding. There is thus the ever present question of whether the method will pay for itself by the gains to which it leads. And we can have no certainty that the answer will be the same for all species in all circumstances.

SECTION K

THE GENETICAL STRUCTURE OF PLANT POPULATIONS

ABSTRACTS of Papers read on MONDAY, 13th SEPTEMBER

THE GENETICAL STRUCTURE OF PLANT POPULATIONS IN RELATION TO GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTIONS

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Kew

The extensive and intensive studies now being completed on numerous populations of a limited number of species of the European flora have revealed an unexpected wealth of variation in structure and behaviour. Some of the variations are common, others are rare ; some have obvious positive and general survival value, some are more or less lethal or harmful, some appear to be neutral from the standpoint of survival within any population ; some are correlated with local environments, some have wider geographical ranges. Hybridisation experiments have shown that most of the variations found in the wild are due to genetic differences and that the operation is often by the interaction of a larger or smaller number of determinable genes. Some, however, are not yet fully understood genetically.

Genetical experiments must be combined with field and herbarium studies if the history of the plants is to be satisfactorily elucidated. The value of the information given by cytology varies with the group.

The above generalisations will be drawn from the consideration of a few groups of species which have been studied by combined methods.

INTRAPOPULATION HETEROGENEITY AND THE BREEDING RANGE
OF THE INDIVIDUAL PLANT

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Durham

In addition to reciprocally outcrossing pins and thrums, certain populations of *Primula vulgaris* contain long homostyles which are normally self-fertilised and outcross on to pins. Observation agrees with the theoretical conclusions that homostyles are increasing to about 80 per cent., pins are decreasing to about 20 per cent., and thrums are entirely disappearing. Slow at first, change later becomes quite rapid.

Considerable heterogeneity between different parts of any one such population may exist. A few yards only may separate groups with constitutions so different that they represent evolutionary stages many generations apart. Such large differences cannot have arisen in one generation by chance from a homogeneous population, but must have been so initiated at an early stage. One section of the population reached the stage of more rapid change, the difference then becoming amplified. But it could not even be maintained with free distribution of pollen between the divergent groups, even though homostyles are self-pollinated.

The breeding range of the individual *P. vulgaris* must therefore be only of the order of a few yards, and a single population cannot be considered as a continuous interbreeding unit. Discussion of the significance of this for general evolution theory must take account of the abnormal rapidity of homostyle evolution.

POPULATIONS OF CULTIVATED PLANTS

A. J. BATEMAN

Bayfordbury

Populations of cultivated plants are simpler in several respects than natural populations. Their study can therefore help to illuminate the even more complex situation in wild plants.

The main factor determining population structure is the breeding system. Subordinated to this are selection intensity, population size and gene dispersal.

The breeding system determines the free and potential heritable variation and the rate of liberation of potential variation. Cultivated plants show a continuous range in breeding systems from self-incompatibility and dioecism giving full outbreeding, to regular self-pollination and vegetative reproduction, giving full inbreeding or its equivalent.

Cultivated plants are selected for a special environment. When human selection is relaxed the subsequent deterioration shows us how natural populations with similar breeding systems will respond to changes of environment.

Population size affects the maximum heritable variation which can be carried and, when very small, the amount of inbreeding in otherwise outbreeding species.

A study of the dispersal of pollen of cultivated plants shows that intercrossing is mainly confined to immediate neighbours, though finite amounts of crossing occur up to large distances. The part which this dispersal plays in determining population structure again depends on the breeding system.

GENE-FLOW BETWEEN INTER-FERTILE SPECIES

H. G. BAKER

Leeds

Attention is drawn to Allan's distinction between *multiform* and *pauciform* natural hybrids. In some cases, natural gene-flow between forms shown to be inter-fertile when crossed artificially appears to be restricted. Recently described cases of this sort are examined. The possible causes of restriction are enumerated and discussed. The stages which may occur in the invasion of a region containing one form by another, closely related and inter-fertile form are outlined and illustrated. An important distinction is drawn between the flow of genes controlling characters of significance in the ecological difference between the forms and those which are neutral in this respect.

INTERSPECIFIC HYBRIDISATION IN *PRIMULA*

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Primrose (*Primula vulgaris*) and Oxlip (*P. elatior*), in certain regions of East Anglia, occur only in woodland; the populations of individual woods are thus isolated from one another. Some woods contain one or other of the pure species, others contain the two species and their hybrids.

Where the species meet, they occupy distinct areas in the wood, probably because of their different ecological preferences. Hybrids are always frequent but they do not outnumber the pure species. From reciprocal artificial crosses, a low yield of viable seeds is obtained, and the vigour of the F_1 hybrids is variable. A somewhat better yield of seed is obtained when the F_1 hybrid is selfed or backcrossed.

There are thus both ecological and genetical barriers which tend to present fusion of the species. It has been suggested that Primrose is replacing Oxlip in the mixed populations, but the available evidence suggests that the condition is one of equilibrium, which may in the course of time shift in one direction or the other as variations of local climate and environment occur.

Efficient barriers of more than one kind separate Oxlip and Cowslip (*P. veris*), and the hybrid between them is very rare. The hybrid between Primrose and Cowslip, which is partially fertile, is of widespread occurrence, but extensive hybrid populations are apparently rare, perhaps because of the marked ecological differences between the species.