

# THE APPLICATION OF GENETICS TO PLANT BREEDING

## I. THE GENETIC INTERPRETATION OF PLANT BREEDING PROBLEMS<sup>1</sup>

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### I. INTRODUCTION

THE influence of the science of genetics on the art of plant breeding has been much less profound than was expected by the early geneticists. For the elucidation of the mechanism of heredity, only factors causing large differences were useful, and it was not immediately realized that these are of little importance in nature or under artificial selection. Progress in the genetic control of small differences has been difficult and slow and many geneticists still consider that minor genes are not worth investigating on their own account. Some genetic principles have been successfully applied by breeders, but often the principles involved are not fully realized, and the application has usually been made with no experimental support beyond deductions from general observations on breeding material. In correspondence on breeding methods it is remarkable how often a practice of fundamental importance is justified by a statement beginning "My feeling is. . . ." It should be the function of the geneticist to substitute objective evidence for the breeder's intuition.

It is the object of this paper to survey the application of genetic theory to cotton breeding in particular and to outline the problems in which the geneticist should be able to help the breeder.

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## II. VARIABILITY AND THE CHOICE OF MATERIAL IN WHICH TO SELECT

Until recently it was generally accepted that the action of natural selection resulted in the purification and propagation of the fittest type in a population. A perfectly adapted type would theoretically be pure, and the existence of variability was usually supposed to indicate recent crossing between pure types (Patel, 1920; Stock, 1927). Recent work on crop populations has shown that the effect of natural selection on variability is very different from what had been supposed. Hutchinson and others (1937 *a*, 1938 *b*) as a result of studies on crop populations in India, concluded that natural selection results in the establishment of a well-adapted population consisting of a great range of types. When grown in pure culture these types differ so much in yield that it is necessary to postulate considerable competition effects to explain their survival in the mixed crop. In most cases the nature of the forces maintaining variability is obscure, but some general observations can be made on such data as are now available. In Central India, American Upland cotton has become established as a permanent component of the cotton crop. In pure culture the indigenous types give a considerably heavier yield. In mixed crops the Upland type gains by competition. The disparity in yield per plant is reduced, and the germination of the Upland is much better than that of the indigenous types. The mixed product is of better quality than the pure indigenous cotton and is preferred by the local mills, and seed from mixtures with the highest proportion of Upland is returned to the cultivators. The lower intrinsic yield of the Upland type is balanced, therefore, by advantages in competition, germinating capacity and quality. In many cases, selective forces vary from place to place in the ecological area. For example, in Central India, cultivators select and grow either yellow grained or white grained *jowar* (*Sorghum durra*) according to personal preference. Selective forces are also likely to vary from season to season as well as from place to place in comparatively small areas, and the effect of such changes in maintaining variability is obvious. It may be concluded that a genetically variable strain will give a more flexible response to environmental variations than a very uniform one. If variability, and not uniformity, is the natural characteristic of crop populations, the breeder's ideal must be reconsidered. Selection for uniformity should not proceed beyond the stage needed to ensure a satisfactory grade in the marketable product, except where it is possible by further specialization to achieve closer adaptation to local climates. Where seasonal fluctuations are of most importance, as for instance in

Tanganyika and Queensland, the maintenance of some genetic variability is a definite item in breeding policy. In the Sudan, on the other hand, place to place variations are such that progress has been made by breeding special strains for different localities (King, 1938). The U 4 variety of Upland cotton in its original variable form proved well adapted to a wide range of conditions in Africa, and selection work has been carried out on it at a number of centres. Local adaptation has become so pronounced that there is now little exchange of substrains between breeding stations and such material as has been exchanged has failed to compete with local selections (Peat & Prentice, 1939).

In early line breeding work it was assumed that the ideal was a "pure line", and once this was established all that was necessary was to preserve it from contamination by mixing or hybridization and it would remain pure indefinitely. Experience with Sea Island cotton in the West Indies shows that this ideal is in practice unattainable. The rate of mutation in certain major genes is high enough to cause serious contamination in a comparatively short time. General deterioration in quality occurs unless there is a constant renewal of the seed supply from selected stocks, even in islands where no cottons exist save the single pure strain under cultivation. The superfine Sea Island strains are very different from what would have arisen in nature, and in the absence of selective breeding, natural selection rapidly changes the strain characteristics.

All cotton breeding experience supports the view that variability is the natural state of unselected populations, and persists in some measure in even the most closely bred pedigree stocks. Degeneration has been most rapid and most serious in the best and most closely bred varieties. Unselected variable "land races", on the other hand, maintain their characteristics unchanged indefinitely. It is a fair inference that the behaviour of a strain depends on selection pressure and not on variability, and the effort at present devoted to achieving purity may profitably be used to increase the efficiency of selection.

Vavilov (1935) and other Russian botanists have studied the distribution of variability in cultivated crops and have postulated a limited number of comparatively small areas where most of the world's crops have been evolved. In these areas, which are usually mountainous and therefore divided into many comparatively isolated pockets, they found that variability is extremely high, and it diminished, usually by the progressive loss of dominant genes, from the centre of origin to the periphery of the distribution. In areas where a species has undergone rapid multi-

plication and extensive distribution secondary centres of variability may arise. In cotton the situation is not always as simple as in the cases quoted by Vavilov (Hutchinson, 1938 *a*). The two cultivated American species have their centres of variability in the two centres of crop variability postulated by Vavilov (1935) in Central America and in the Cordillera-Andean ranges of Colombia, Ecuador and Peru. Of the cultivated species of the Old World, *Gossypium herbaceum* appears to have its primary (though less important) centre of variability in the savannah countries of West Africa, with secondary centres more important than the primary one in Western India and in Iran, Afghanistan and Russian Turkestan. In *G. arboreum* there are at least four centres of variability, in the Sudan, South India, Assam and East Bengal, and eastern Burma and Indo-China. The discovery that most of the variability in a species is to be found in a small fraction of its total range, is of great value both in interpreting past breeding problems and in guiding the choice of breeding material. The value of material from areas of high variability has been stressed chiefly by workers in countries outside those areas, and they have built up large collections of types as reserves for future breeding work. Recently there has been a tendency for countries such as India where the variability is great to follow the Russian example. It should be obvious that no collection of types can compete with the untouched native variability of the cultivator's field, and where there are rich indigenous variable crop populations it is more important to see that they are maintained than to build up large type collections.

Recently Mason (1938) has commented on the lack of success in synthesizing new strains of cotton from hybrid material. In India, to which Mason's remarks particularly referred, there are two centres of variability of *G. arboreum* and one of *G. herbaceum*, and it is therefore natural that the exploitation of existing variability has taken precedence over selection in hybrid material. The United States cotton belt, on the other hand, is outside the area of high variability in *G. hirsutum*, and the variability required for breeding work has been more frequently found in hybrid stocks. In Egypt also, where *G. barbadense* is not indigenous, hybrid material has been found to be the best source of variability (Brown, 1939).

Apart from the high variability of unselected local cotton crops, the use of hybridization as a source of variable material has been discouraged in India by repeated failure. The causes of failure have been elucidated by Harland's (1936) analysis of the genetic nature of species differences and the revision of the classification of the genus in the light of genetic

results (Harland, 1932; Hutchinson & Ghose, 1937 *b*). Harland's work was chiefly with the two New World cultivated species, *G. hirsutum* and *G. barbadense*. He showed that though they cross freely and give a very vigorous  $F_1$ , homologous characters are built up in such widely different ways that the genetic balance is disintegrated by segregation in  $F_2$  and later generations. Vigorous and productive selections are almost invariably multiple heterozygotes which segregate into a welter of types, the majority of which are inferior in vigour and productivity and often morphologically abnormal. Harland (1936) further showed that it was possible to transfer single genes or small groups of genes from one species to another without disturbing the species balance. He concluded that improvement by interspecific hybridization is to be looked for through the addition of small groups of genes from one species to the complement of the other, and not through breeding intermediate types. The revision of the classification of the cottons of the Old World by Hutchinson & Ghose (1937 *b*) made it possible to examine hybridization experiments with Indian cottons in the light of Harland's theory of species balance. It was found that those crosses with which success had been achieved were between types regarded on genetic grounds as members of a single species (*G. arboreum*). Those from which no satisfactory types had been isolated were from crosses between *G. arboreum* and *G. herbaceum*, which are genetically distinct species. In breeding work with such hybrids, vigorous productive selections were shown to be multiple heterozygotes which broke down into a range of unproductive, often unbalanced types. The conclusions drawn from experimental hybrids were confirmed by field studies of crops in which the two species are normally grown mixed. Although hybridization occurs and  $F_1$ 's, by reason of their hybrid vigour, are the outstanding plants in the crop, later generation hybrids are rare or absent, and there is no tendency whatever for the species distinction to disappear.

No breakdown has been observed in intervarietal or inter-strain crosses, though intervarietal diversity in the genetic basis of important lint characters has been demonstrated by Silow (1939). Hybrid material that does not transgress species boundaries can be confidently recommended to breeders for straight selection. Among the Asiatic cottons two of the most promising lines of improvement in *G. arboreum* are selections from hybrids between northern Indian and Chinese forms and between northern and southern Indian forms. These have been shown (Hutchinson & Ghose, 1937 *b*; Hutchinson *et al.* 1938 *c*) to involve differences of approximately varietal rank. Among New World cottons, hybrids of

*G. hirsutum* × *G. hirsutum* var. *religiosum* are likely to be of value for selection under African conditions.

With the understanding that success will be dependent upon rapid re-establishment of the genetic balance of one or other species, the plant breeder may now return with some confidence to interspecies hybridization. Considerable success has already been achieved by Knight & Clouston (1939) in transferring the "blackarm" (*Bacterium malvacearum*) resistance of a strain of *G. hirsutum* to an Egyptian type of *G. barbadense*. They backcrossed the interspecies  $F_1$  three times to the Egyptian parent, selecting rigorously in each segregating generation types with  $F_1$  resistance and as nearly as possible the morphological characteristics of the Egyptian parent.

### III. THE IMPROVEMENT OF THE EFFICIENCY OF SELECTION

In the earliest days of cotton breeding Balls (1919) emphasized the importance of the components of yield. Through his work in Egypt and Harland's (1920) in the West Indies, it has become an accepted practice among breeders to study such components of yield as bolls per plant, seed cotton per boll, seeds per boll, lint per seed, etc. It soon became evident that the effects of environmental fluctuation were much greater on some characters (e.g. bolls per plant) than on others (e.g. seed cotton per boll) and it followed that selection on the latter group is much more effective than on the former. Improvement of the comparatively stable components of yield results in improvement in yield up to a point. Beyond that point the gains due to selection are compensated by depreciation in characters beyond the reach of selection. In the Heaton strain of Sea Island cotton lint index (weight of lint on 100 seeds) has been raised 30 % or more by selection and the greater part of the improvement is reflected in increased yield. Selection in the same strain for high weight of seed cotton per boll has given an improvement which is not reflected in a higher yield. Similar selection in an Upland cotton has resulted in a very large boll, and a disproportionate reduction in the number of bolls per plant. The common experience that intensification in one character can only be obtained at the expense of others is often the result of physiological incompatibilities. Even when there is no physiological barrier to combination, the chance of getting the maximum expression of character *B* in a plant selected for intensity of expression of character *A* is very small. Until the relative importance of these two possibilities is known no estimate can be made of the probable limits to improvement by selection. What is now required is a detailed physio-

logical-genetic analysis of the interrelations of the component characters of the plant. The organism is an integrated whole and it is obvious that any large change in one character must either be accompanied by corresponding changes in other characters, or disturb the balance of the plant. Change under selection should therefore be co-ordinated change, and not merely intensification of a single character.

Variation is of two kinds, environmental and genetic, and selection will be most efficient when the ratio of the genetic component to the total variance is at a maximum. The first great improvement in selection efficiency was the substitution of selection in progeny rows for mass selection. This is generally regarded as an application of the pure line theory, but its success is due to the fact that selection is more efficient when based on progeny means than on single plants. Between progenies the environmental component of the variance is less, and the genotypic component more than between plants.

Later attempts to improve the efficiency of selection have been concentrated on the problem of reducing the environmental variance in breeding material. In the "Purity Chequer" used in Egypt (Brown, 1932) environmental effects are reduced by replication. The plots are arranged systematically and every effort is made to provide optimum conditions for growth and development. No yield comparisons are made, but the seed cotton is examined for lint and seed characters. The data are analysed by correlation tables ("target diagrams"), and selections are made in progenies that combine high mean values and high variances in desirable characters. The weakness of the Egyptian system is that there is no attempt to evaluate yield characteristics in the early stages. Another systematic arrangement is that devised by Trought (1934) in which a line of the strain under test is compared with two lines of control, one on either side. As each comparison involves one line of the strain, two of the control and two guard rows, only one-fifth of the total area used is occupied by the material under test. Yield comparisons are made on a single plant basis with elaborate precautions to ensure that plants are only compared with exactly similarly spaced plants in the control rows.

Experimental designs involving randomization as well as replication were applied to progeny row breeding material by Hutchinson & Panse (1937 c), and have proved very successful in reducing the environmental contribution to the variance. The long delay in adopting modern statistical methods was probably due to the belief that a satisfactorily low error could not be expected with small plots. It does not appear to

have been realized that the very fact that progeny row selection has been successful shows that the differences between progenies are in general greater than can be ascribed to chance environmental fluctuations. It was therefore to be expected that the equalization of the major environmental differences by replication and arrangement in blocks would result in improved efficiency, even though very small plots were employed, while randomization to allow of the calculation of an estimate of the error of the progeny comparisons is obviously desirable.

TABLE I  
*Standard errors in randomized block experiments with  
breeding material of Montserrat Sea Island cotton*

Column ... ..	1		2		3		4	
	Experimental error expressed as coefficient of variation		Experimental error including block variation %		Block efficiency		Standard error of any strain mean %	
	Progenies	Bulks	Progenies	Bulks	Progenies	Bulks	Progenies	Bulks
Germination	23.8	—	24.8	—	1.09	—	7.53	—
Final stand	—	5.8	—	7.9	—	2.26	—	2.37
Node number	5.3	—	7.0	—	1.80	—	1.67	—
Days to first flower	3.2	—	4.6	—	2.04	—	1.42	—
Boll loculi	3.4	—	3.5	—	1.06	—	1.07	—
Bolls per plant	18.0	12.0	21.9	14.7	1.48	1.50	5.69	4.98
Seed cotton per boll	6.8	2.1	7.1	3.8	1.10	3.23	2.15	0.86
Seed weight	3.8	2.4	4.6	3.4	1.46	1.95	1.20	0.98
Lint index	4.9	3.3	6.4	4.3	1.69	1.75	1.55	1.35
Ginning %	4.3	2.7	4.8	3.5	1.26	1.73	1.36	1.10
Lint length	1.9	1.1	2.6	1.6	1.80	2.34	0.60	0.45
Yield of seed cotton	—	9.8	—	15.7	—	2.56	—	4.00
Yield of lint	—	10.0	—	14.6	—	2.15	—	4.08

The efficiency of selection in randomized block layouts with cotton may be illustrated from a progeny row trial and a small bulk trial of M.S.I. cotton in Montserrat in 1938. In the progeny row trial there were twenty single plant progenies in an experiment with ten blocks divided into five plant plots. In the small bulk trial there were twenty single progeny bulks (i.e. second generation from single plants) in an experiment with six blocks in which the plot size was 72 hills with one to two plants per hill. The efficiency of the experiments for each of the characters studied is summarized below (Table I). In the first column is given the coefficient of variation, evaluated by expressing the square root of the error variance as a percentage of the grand mean. Column 2 contains an estimate of the experimental error when the randomized block layout is ignored and the estimate of the error variance includes the effects of

fertility differences between the blocks. This error variance was calculated from the sum of squares for blocks + error, divided by the appropriate degrees of freedom. The square root of the resulting variance is given as a percentage of the grand mean. The best estimate of the efficiency of the block arrangement is the ratio of the reciprocals of the variances used in calculating the data in columns 1 and 2. These ratios are given in column 3. Finally the efficiency of comparisons between strain means is given in the last column by the standard errors of the means of ten plots in the progeny row trial and of six plots in the small bulks trial. These again are expressed as percentages of the grand mean.

The elimination of block differences resulted in large increases in accuracy in most characters. Not only does such a design improve the accuracy of comparison. It gives reliable guidance on which characters can be most profitably subjected to selection. As a group, seed cotton and lint characters were accurately estimated, differences of the order of 5 % being detected with confidence even with five plant plots replicated ten times. Yields and bolls per plant were much more variable, the larger plots six times replicated only providing satisfactory evidence of the existence of differences of the order of 12-15 %. The accuracy is of much the same order, however, as that obtained in properly replicated variety trials, and is therefore satisfactory, in that the small plots have not greatly increased the variability.

There are serious disadvantages inherent in progeny row breeding, especially for areas in which wide fluctuations in soil and climate occur. With the small amount of material available and the detailed examination to which it is subjected, it is impossible to carry out tests under a representative range of conditions. To improve the accuracy of his comparisons the breeder usually chooses uniform, fertile fields for his trials, and thereby exposes himself to the criticism that his strains have been bred and tested for suitability to a set of conditions which does not exist in practice. Plant habit, proneness to lodge under a heavy crop, resistance to certain pests and diseases and so on, can only be estimated in large plots. Such characters as ability to give a fair yield even under bad conditions, and satisfactory response to the range of soils and seasons likely to be encountered are particularly important in countries with uncertain climates and wide ranges of soil conditions, as for example South Africa and Queensland. To meet these problems breeders reduce progeny row work and bulk up their material as quickly as possible for extensive testing. The greatest successes of progeny row breeding in cotton have been attained in countries with comparatively uniform climates, such as

the West Indies and Egypt. In this connexion Mason (1938) has suggested that "secondary" selection, which may be defined as selection in the immediate progeny of single plants, has been considerably over-emphasized at the expense of "primary" selection which includes single plant selection in unselected populations, hybrid material and improved bulks multiplied up from earlier selections. He pointed out that most of the outstanding successes in cotton breeding in India and Africa have been due to "lucky finds" and not to steady progress in orthodox breeding plots. One very important reason for this is that in new cotton-growing countries, or where a new and powerful factor is introduced into the situation, such as the invasion of a disease or pest, the breeder can sample a variable crop population with a reasonable expectation of making considerable progress in a short time. Also, until the development of the randomized progeny row technique, the testing of breeding material was so inefficient that the small differences on which steady improvement under selection should be based were only detected with difficulty. Under the circumstances secondary selection has been as successful as could be expected, as for example in the production of a steady improvement in lint and seed cotton characters under the comparatively uniform climatic conditions of Egypt and the West Indies.

#### IV. DISCUSSION

There can be no response to selection unless the material is genetically variable. The relation of variability to rate of change under selection, and the effect of selection in reducing variability are therefore fundamental factors in breeding theory. The examination of unselected crop populations has provided information on the equilibrium between selection and variability that is established in nature, and it appears that variability persists at a high level. It follows that natural selection does not necessarily result in uniformity, and the stability of such mixtures must be due to selection and not to genetic uniformity.

The records of breeding projects with Sea Island cotton show that it is in practice impossible to achieve genetic uniformity, even when it is deliberately sought. Variance may be greatly reduced, but it persists in some measure in even the most closely bred strains. If the stability of unselected populations is due to selection and not to genetic uniformity, the breeder may regard purity as a secondary consideration, and a new approach to his problem is possible.

The problems involved in the choice of material for selection have been better studied than most others that face the breeder. For most

crops the areas of high variability are known. Now that it is recognized that hybridization is only a means of increasing variability, and is a preliminary to selection and not a substitute for it, breeding programmes are better planned. No one nowadays wastes his time creating variability when it exists in his neighbour's fields. Where hybridization is necessary, genetic investigations have marked off the dangerous areas where cytological abnormalities and interspecific breakdown require special treatment, and in some cases, as in cotton, sound guidance can be given as to the type of variability and the order of its magnitude likely to be found in hybrids of any given type.

The chief importance of the application of modern statistical layouts to progeny row material lies in the demonstration that breeding material can be subjected to rigorous tests at any stage beyond the single plant. Early testing is obviously a great advantage for some characters. When, for example, certain minimum lint characters are required in a cotton strain, all progenies failing to reach the standard can be discarded immediately, enabling a more rigorous selection to be exercised for yield and flexibility of response when the remaining material has been bulked up. There is now no excuse for uncritical breeding work. It is possible to determine for each character the earliest stage at which efficient selection and critical comparison can be made, and a programme of progressive sifting and testing can be built up. The argument that flexibility is of prime importance is no excuse for inefficient testing.

In these problems considerable progress has already been made. There remain lines of enquiry more specifically genetic in the narrow sense on which work has hardly been started. The analysis of yield into its components was one of the early advances in cotton breeding. Its logical counterpart, studies of the synthesis of yield under different circumstances and in different strains, has hardly been touched. The development of discriminant functions (Fisher, 1936; Fairfield Smith, 1936) provides a tool with which the study can be undertaken. At present there is some knowledge of what characters can most easily be influenced by selection, but nothing is known of the extent to which a change in one character will result in compensating changes, which may perhaps be less easily detected, in others.

Studies of the rate and magnitude of change that can be induced by selection have an obvious bearing on breeding policy, but little information is available beyond "Student's" (1933) analysis of Winter's selection experiment, Harland's (1934) account of the breeding of Montserrat Sea Island cotton and Hutchinson & Kubersingh's (1936) analysis of the

effect of selection on Malvi cotton. A preliminary enquiry into another aspect of the problem of the mass action of genes is Anderson's (1939) recent calculation of the limiting effect of linkage on gene assortment in distant hybrids. This has an interesting bearing on the rate of re-establishment of the species balance in Harland's backcrossing method of exploiting interspecies hybrids.

Enough has been said to indicate the great range of fundamental problems facing the plant breeder. Many of them fall outside the scope of genetics as the subject is now studied, and it is one of the attractions of the attempt to develop an applied branch of genetics that the stimulus of practical needs opens up lines of enquiry of wide theoretical interest.

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