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Genetical Bases of Plant Breeding

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When I was first honoured by your invitation to give this lecture, I naturally gave a good deal of thought as to what the subject should be. Rubber was an obvious choice but I had to reject it since, unlike everybody else in this room, I know almost nothing about it. Finally, I chose *Genetical Bases of Plant Breeding* in the belief that all plant breeding programmes, however successful at the empirical level, are the better for genetical understanding and in the belief also that genetical understanding is sometimes critical for plant breeding progress.

I want to make three very general points about plant breeding first and then go on to a little more detail. First of all let me remind you of the crucially important fact that plant breeding is economical. It is simply the cheapest and most economical thing which we can do to ensure further progress in a reasonably advanced agriculture. Conversely, agricultural progress is very commonly dependent upon advances in plant breeding for the practical realisation of other technological advances. As to economy, various recent calculations in Britain have shown that the returns on investment in breeding a successful variety is of the order of many thousands of times the initial cost; profits are measured in millions. Both these statements could well be illustrated by reference to rubber. Second, plant breeding is a curious mixture (as with so much of our applied research) of technology and science. It has scientific (that is, genetical) foundations but it is also a technology and has to be approached as such, with what one might call an 'operational research' style of attack. Third and finally, plant breeding on a scientific basis has a history of only about fifty years. Plant improvement has been going on ever since man

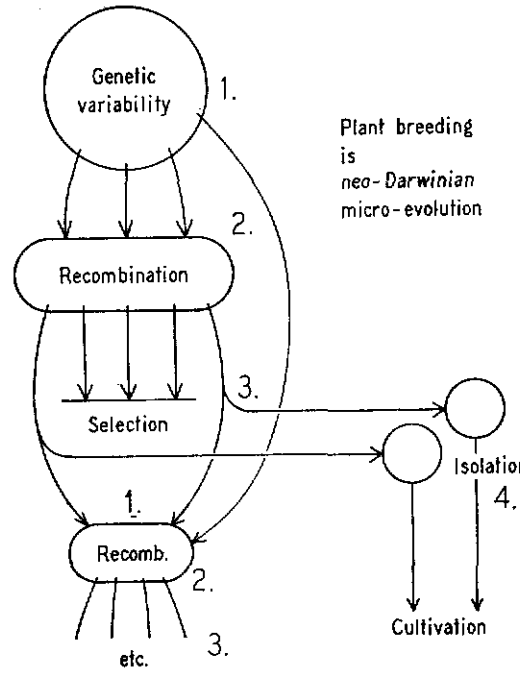

Figure 1. The four phases of plant breeding.

first practised agriculture, say for eight or nine thousand years; conscious plant breeding has been going on for perhaps one hundred and fifty years. Scientific plant breeding, *i.e.*, plant breeding on a genetical basis, has been going on only since the essential genetics started to become understood — for the last fifty years.

From those generalities I want to go on to a discussion of seven points which collectively seem to cover the main features of the subject.

SEVEN POINTS ABOUT PLANT BREEDING

1. Neo-Darwinian Micro-Evolution

My first point is an assertion and it is that plant breeding is essentially neo-Darwinian micro-evolution. *Figure 1* makes the point that

there are four essential elements in both neo-Darwinian micro-evolution and in plant breeding, namely: (i) generation of genetic variability; (ii) genetic recombination among that variability; followed by (iii) selection; and, finally, (iv) isolation. These are the essential steps in micro-evolution as we understand it at the present time and they are also the essential steps in any plant breeding programme. The plant breeder in fact is an evolutionist, bending populations genetically towards new norms of adaptation. Notice that all these four steps are essential, both for evolution and for plant breeding. Progress is impossible without the operation of all four of them and yet it is, I think, a historical fact that nearly all the effort that goes into plant breeding programmes tends to be concentrated on the last two phases of the sequence rather than to be distributed over all four. Attention is thus concentrated upon the selection and isolation phases to the neglect of the management of variability and recombination. For example, most inbred cereal breeding programmes seem to be almost designed to minimise genetic recombination, although it is evident both from first principles and from experiment that this phase is of crucial importance. Similarly, an enormous amount of plant breeding goes on without any serious consideration of the starting materials. I will come back to this point later in a slightly different context. Meanwhile, it must be true that, unless the right material goes in and unless recombination is adequate, the desired recombinants will not be available for selection.

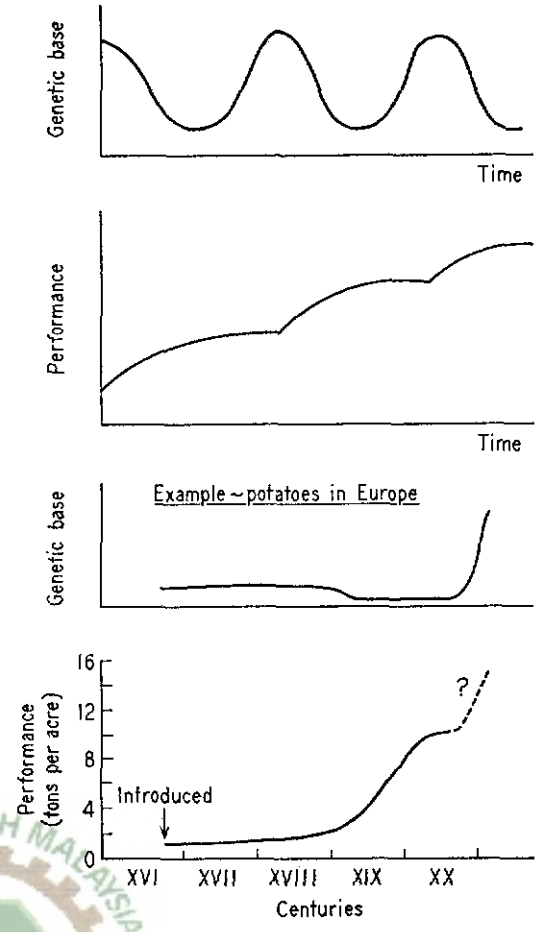

Figure 2. The genetic base and performance.

2. *Adaptation and Genetic Base*

My next point is illustrated in *Figure 2*. Adaptation, that is, net genetic change in response to selection, carries with it a seeming paradox which might be called 'the more the less principle'. Starting from any given genetic base, the greater the progress, the less the potential for further progress. This follows from the fact that all adaptation involves a narrowing of the genetic base, a discarding of genetic material; that is what selection is about. One cannot have selection without some genetic destruction. And the more successful the selection, the better the adaptation, the less the variability that remains and the less the potential for further advance. Many selection experiments, particularly on favourable organisms such as *Drosophila*, but convincingly also in less favourable organisms such as hens and maize, support this idea. What generally happens is that, in any restricted population, prolonged selection gives, at first, rapid gains which diminish and finally come to a plateau beyond which no further advance seems to be possible. Sometimes there are secondary advances in such experiments which are usually interpreted as meaning either that favourable mutations have occurred or that certain rare

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recombinants have been recovered. The details are often rather hard to interpret but the point I want to make is that the *Drosophila* experiments are carried out on a scale and with a refinement of technique that are not generally possible in plant breeding. So the plant breeder will usually be well advised in practice to take a poor response to selection as a signal to renew the genetic base.

The top part of *Figure 2* is a general and rather theoretical diagram in illustration. As selection proceeds and performance rises, so the material comes to a plateau and the genetic base is correspondingly narrowed; this is followed by a new injection of variability and a new rise to a new plateau and so on. It is hard to illustrate this principle in detail for many crops, but this sort of pattern is surely a frequent one, a cycle of response following the introduction of new variability. Patterns in practice are of course much more complex than in this simple theoretical diagram and this is illustrated for the potatoes at the bottom of the *Figure*. Potatoes were introduced from South America to north temperate countries in the sixteenth century and were at first very poorly adapted. Two hundred years of slow progress were followed by a hundred years of very rapid advance during the nineteenth century in which the yield of the crop increased fivefold; thereafter a plateau was reached and potato breeding has had remarkably few major successes throughout the world for the last fifty years. This situation reflects a severe narrowing of the genetic base and thus limitation upon further advance. New variability is wanted and this, it is fairly certain, we shall be able to provide by having recourse, for a second time, to the South American ancestral stocks. Work along these lines, developed in Britain but now being taken up elsewhere, should show in a few years whether the interpretation is correct and the remedy well chosen.

To summarise, the adaptation paradox states that 'the more now the less in the future'. Clearly, the plant breeder must continually look to the genetic materials with which he is working if the consequent 'stop-go' cycles are to be avoided.

3. *Inbreeding and Outbreeding*

My third point is summarised in *Figure 3* which shows that breeding and propagation systems of our crop plants determine breeding plans. There is a broad contrast between inbreeding and outbreeding species. Inbreeders tolerate homozygosity and so can be bred as pure lines; outbreeders must maintain heterozygosity; hence controlled hybrids. But clonal propagation can cut through some of the complexities of outbreeding systems. Thus, in an outbreeding annual such as maize, we need rather elaborate inbreeding and hybridisation schemes whereas, in an outbred clonal plant (*e.g.*, potato, rubber and sugar-cane), it is possible to fix desirable heterozygotes in one step by making clones of them. To this extent the breeder of an outbred clonal plant is much more favourably placed than the breeder of an outbred annual. Perhaps the most unhappily placed breeder of all is he who works with outbred long-term woody plants which cannot

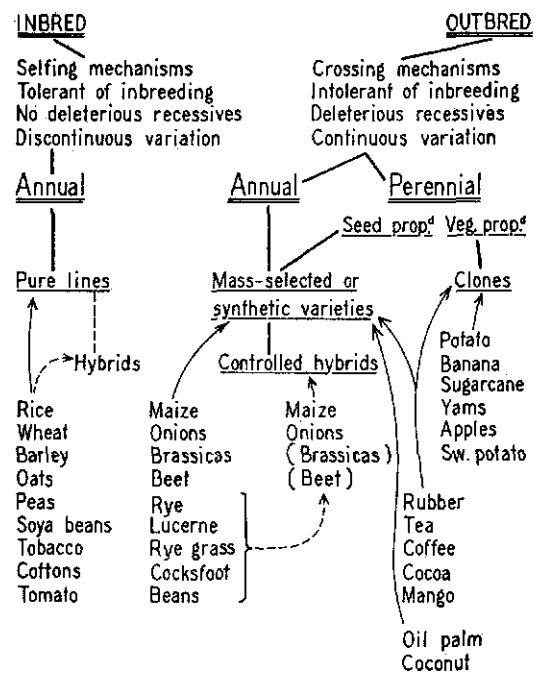


Figure 3. Breeding and propagation systems in crop plants.

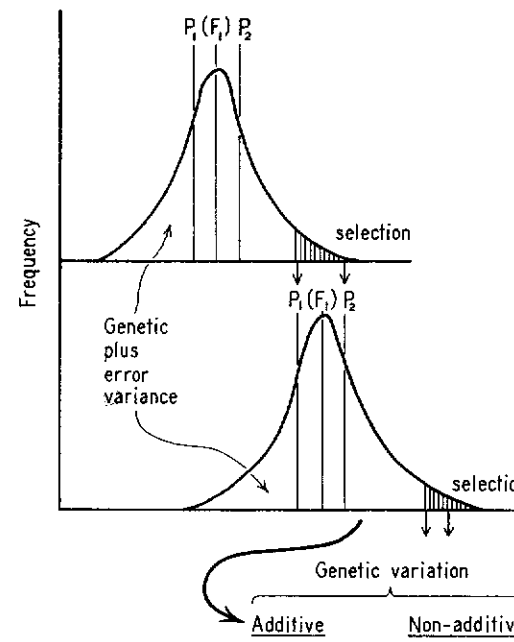
be cloned, for example, coconuts and oil palms. The generalisation here, then, is that the breeding system (reflected broadly by separation into inbred and outbred) *plus* the propagation system (whether propagated by seed or by vegetative material), determines the methods, the general approach and the possibilities open to the breeder.

Notice, by the way, a second point, and a rather interesting one — the strong correlation between breeding system and habit. Broadly, our annuals tend to be inbreeders, our perennials to be outbreeders. Darwin knew about this relation and suggested that it reflected an adaptation to seed setting by annuals in isolated environments. There is little doubt that, in addition, our plant breeding habits have quite often intensified inbreeding in annual crops.

All this has a rather important consequence. The use of inbred annuals and of clones in vegetatively propagated perennials tends to lead to situations in which large areas are covered by either pure lines (as in the cereals) or by clones (as in sugar-cane, banana and rubber). The temptation to keep very few excellent cultivars and to reduce the genetic variability in the breeding pool is more or less overwhelming so that, for inbred annuals and clonal perennials, the narrowing of the genetic base, always a general tendency in plant breeding, is particularly acute. One immediate result is to encourage disease. In the U.S.A., STEVENS (1948) showed that clonal and inbred crops suffered more severely from diseases than did the more heterogeneous outbred seed-propagated populations. This does not mean that the use of pure lines and clones should be abandoned; it merely means that, for crop plants bred and propagated thus, we need to take special precautions to preserve the genetic base and we ought to be aware of the inherent risks. The 'Hungry Forties' of Europe in the mid-nineteenth century were hungry because a restricted population of potato clones was decimated by a new disease, Blight, to which it was not adapted. In cacao and rubber, by contrast, there has been some understanding of the desirability of spreading risks by growing both clones and seedlings.

4. Polygenic Variability

Figure 4 takes us into a new topic and this is my fourth point, namely, the general question of the place of biometrical genetics in plant breeding. Nearly all the characters with which the plant breeder has to deal are polygenic. They are not determined by simple, straightforward, Mendelian-style major genes but rather by relatively large numbers of genes of small effect, which cannot be handled by Mendelian techniques but must be treated conceptually by biometrical genetical methods. A great deal of effort has gone into biometrical analysis of information from experiments on polygenic characters, with the aim of sorting out the kinds of gene action concerned. I

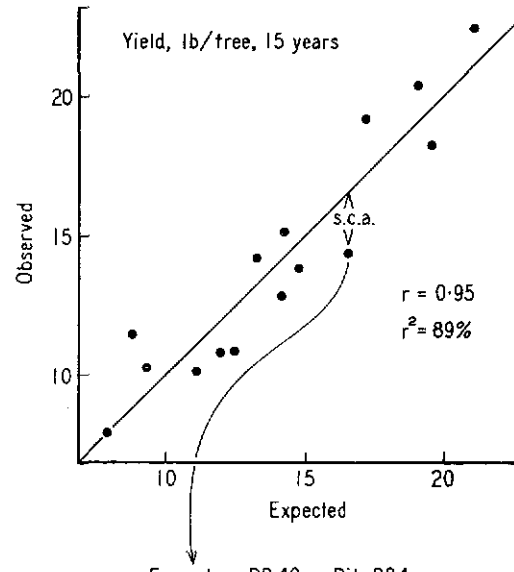


	Additive	Non-additive
Selection	effective	less effective
Response	rapid and continued	slow and restricted
Family performance	predictable	unpredictable
Phenotype and breeding value	correlated	not correlated
Polycrosses	useful	not useful

Figure 4. The importance of additive genetic variation.

believe that most students would agree that many of these efforts have been fairly unrealistic; they have attempted to go further than the information reasonably allows. On the other hand, it is generally accepted that at least a broad division of polygenic variability into an additive fraction and the rest is useful and valid. The dispute only arises as to what should be done with the rest. For the plant breeder, this differentiation between additive variation and the rest does seem to be of importance, because it is the additive fraction which determines ready response to selection; it is the easy, practical bit, one might say, of polygenic variability. *Figure 4* summarises the point and shows an exceedingly simple situation, one in which a segregating population yields a selected fraction (the shaded corner of the distribution) and the process is repeated generation by generation. This is the situation that obtains when the character selected is both highly heritable and additively determined, so that the mean of one generation corresponds rather exactly with the mean of the corresponding parental fraction. From the bottom of *Figure 4* we see that, in these circumstances, selection is effective, response is rapid and continued, family performance is predictable and the phenotype of a parent and its breeding value are correlated. By contrast, when the additive fraction is small, selection is less effective, response is at best unreliable, family performances are unpredictable and progeny tests are essential to determine breeding value. In short, the size of the additive fraction determines breeding plans; a large fraction makes life vastly easier for the plant breeder.

Figure 5 gives a concrete illustration. The data are yields of 15 (5×3) rubber families from ROSS AND BROOKSON (1966). Expected yields are calculated from marginal totals on the basis of simple additivity. Thus to each parent is assigned an additive breeding value or General Combining Ability (G.C.A.) and the deviation of observed from expected represents the unexplained remainder, a compound of error and non-additive genetic effects or Specific Combining Ability (S.C.A.). The agreement is remarkably close, so G.C.A.



Example — PB49 x Pil B84

General mean	14·2
PB 49, GCA	+ 4·9
Pil B84, GCA	− 2·6
Expected	16·5
SCA	− 2·1
Observed	14·4

Figure 5. General Combining Ability (G.C.A) for rubber yields based on data of ROSS AND BROOKSON (1966).

accounts for most of the differences between family yields. The implications for rubber breeding are direct and important. GILBERT (1967) has recently shown that this approach can be generalised and even very unsystematic plant breeding data made to yield analyses of great importance for the guidance of breeding programmes.

The use of correlations deserves comment at this point. A great many plant breeding programmes have various assumptions about correlations built into them. Ideally, we should always select directly for the character with which we are concerned; for example, if we were breeding forage plants, we should test all our materials by feeding them to animals and determining their value in terms of animal production. In practice this is impossible. Instead, we generally make the assumption

that dry matter yields, supplemented by chemical analyses, are directly related to animal feeding value and proceed on this basis. Plant breeding is full of this sort of situation in which we select, not on the character itself, but on simpler characters which we either know or assume are correlated and on which selection can more easily be practised. The correlations do not even have to be very high: GILBERT (1961) showed that even low correlations, so long as large numbers were involved, could be remarkably powerful in advancing the desired character. Practical decisions have to be taken on an operational basis, the object always being to maximise advance per unit effort expended. This is a point which, I think, deserves more attention than it usually gets.

Finally I should like to make a historical comment. I think it is true to say that plant breeding at large has been surprisingly little informed by biometrical genetical ideas, in contrast to animal breeding, which has been rather strongly backed by excellent biometrical genetics. Why this should be so is not clear but it may be connected with the fact that animal breeding is generally based on rather large and expensive units. It is thus worthwhile to take a lot of trouble to reach the best available decisions. In plant breeding, economy of material is less important; one can afford to be rather wasteful. Whatever the cause, it is surely true that plant breeding, with a few honourable exceptions, has been weak on the biometrical genetic side and that this has been a weakness which deserves remedy.

5. *Oligogenic and Polygenic Disease Resistance*

The fifth point I want to make concerns systems of disease resistance *(Figure 6)*. Broadly there are two kinds of resistance: first, there is the kind brought about by one or a few major genes (or oligogenes), which behave in an ordinary Mendelian way; second, and in contrast, there is polygenic resistance controlled by several genes of small individual effect which obey the same sort of biometrical rules we have just been discussing in a different context. For the moment we will restrict the discussion to disease caused by airborne fungi. As a generalisation, oligogenes conferring resistance to an airborne fungus fail. There are now scores (perhaps hundreds) of examples in potatoes, cereals and other crops to support this statement. What happens is this: the plant breeder breeds a major-gene resistant variety which is immune to the pathogen and is grown in the field on a fairly large scale for some years, at the end of which time the pathogen has readapted itself by mutation and/or recombination to the hitherto resistant host and the final situation is pretty much as it was before. This is illustrated on the top left of *Figure 6*. This situation is now so general as to be accepted as the norm; oligogene resistances bred against airborne fungal pathogens fail in a few years and the history of plant breeding during the past fifty years offers abundant illustrations. By contrast, an efficient polygenic resistance produces a quite different

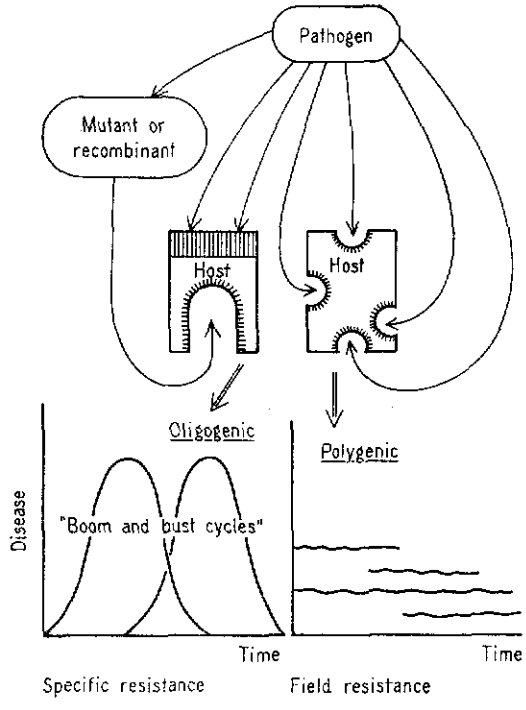


Figure 6. The two patterns of disease resistance.

pattern of response. The host is immune to no strain of the pathogen but is resistant to all; the pathogen is admitted but contained. The result is a fairly constant attack at a level depending on the exact constitution of the host. It is well established that resistance of this kind is indeed constant over a period of years.

The agricultural results are summarised in the bottom part of *Figure 6*. On the left we have what SUNESON (1960) called 'boom and bust cycles'. He coined this phrase in connection with North American cereals, crops in which immunity and epidemic have followed each other in five- or ten-year cycles for the past fifty years. The cereal breeder, running strongly to stay in one place, has generally managed just to keep up with the rusts. The polygenic situation on the right of *Figure 6* is quite different: a steady level of attack characteristic of variety. Cereal breeding is still operating on the 'boom and bust' pattern; potato breeding in recent years, however, has moved over nearly entirely to polygenic resistance, which has now been understood in the crop for a dozen or so years. In time, no doubt, oligogenic specific resistances to airborne fungi will be a thing of the past; polygenic 'field resistance' is harder to handle but it is much more stable and effective. VAN DER PLANK (1963) refers to these resistances as 'vertical' and 'horizontal' respectively.

I have been speaking so far about airborne fungal pathogens, and these generalisations hold very well for them. As to diseases caused by bacteria, viruses, soil-borne fungi and nematodes, the same generalisations hold in principle but certainly do not work so dramatically in practice. Details, I think, lie outside the scope of this lecture. We will simply note that oligogenic resistances to these diseases are commonly much more effective and stable, but that there have been scattered examples of the so-called breakdown situation and there will no doubt be many more.

6. *Heterozygosity and Heterogeneity*

The next point I want to make concerns heterozygosity and heterogeneity. We are familiar with the idea that in the outbred seed-propagated crops, such as maize and brassicas and, to a lesser extent, in the outbred clonal crops, such as potatoes and rubber, heterozygosity makes a significant contribution to performance and stability of performance in the field. There is also a great deal of evidence from animal work (for example with *Drosophila* and chickens) that exactly the same applies in animal populations. Unfortunately our genetical understanding of what is involved in heterosis is still rather weak. The subject is extremely complex and discussion of it lies outside the scope of this lecture. However this may be, many very successful breeding programmes have long been aimed at producing high levels of heterozygosity in producing populations. Maize, of course, is the classic case. In outbreeders, therefore, heterozygosity is of unquestioned importance both for performance and stability.

Now, it has long been assumed that inbreeders (for example the wheats and barleys) do not react to heterozygosity in the same sort of way as outbreeders, that is, they do not show heterosis. Nevertheless there is now much evidence that this is wrong and, therefore, our habit of breeding inbred cereals by means of pure lines may have been ill-founded. As a result, there is now a strong interest developing, mostly in the United States but to some extent also in Europe, in the possibility of converting our traditional inbreeding cereals into hybrids at the field level, as tomatoes have already been partly converted. Whether this will be practicable or not is a difficult question, the answer to which will depend upon technical problems of hybrid seed production. Unfortunately, there is some muddled genetic thinking in this context. The fact that one can demonstrate high levels of performance in hybrid cereals is not of itself evidence that it is desirable or necessary to breed such plants by means of F1 hybrids. There are important genetic problems here to which we simply do not know the answers. It may be that the evidence of F1 heterosis in the cereals should be taken to indicate that we need new and more refined methods of breeding inbred lines rather than moving towards hybrids.

An analogous component of performance and stability is heterogeneity, and this is a feature of our crop populations which is very largely ignored. In general, advanced agriculture tries to make its populations as uniform and homogeneous as possible. The reasons for this are partly technological and commercial, partly aesthetic and partly bureaucratic but almost never genetical or agricultural. In fact we could, I am sure, tolerate far higher levels of heterogeneity in our crop populations than we generally accept now as being either possible or desirable, if it could be shown that there was any considerable advantage in doing so. Experimentally the evidence in favour of heterogeneity in crop populations is rather strong. For example, work on heterogeneous cereal populations, scattered and fragmentary as it is, collectively shows that combinations of pure lines commonly advance the performance over the average of the components by an amount in the region of 3–5 per cent (sometimes by as much as 10–12 per cent). Mixtures also have a markedly stabilising effect such that interaction variances are reduced as compared with pure lines. The total evidence on this subject is now rather impressive and, yet, we deliberately reject heterogeneity in our crop populations as a means of both increasing and stabilising performance. We have no knowledge of the physiology or ecology of this sort of positive productive interaction.

I think this is an area in which we can expect considerable changes during the coming years, even though there is still much prejudice against heterogeneity and the practical problems will sometimes be formidable.

7. *Multiple Selection*

The seventh and last point I want to make concerns multiple selection *(Figure 7)*. This subject can be regarded as another phase of biometrical genetics. The demands we make on a crop variety are always complex in the sense that we need high levels of expression of a considerable number of characters. In practice, all good plant varieties, even excellent ones, are compromises, certainly in one or two, and often in many respects. The perfect variety has never been bred and never will be; *(a)* in *Figure 7* shows why. It makes the point that multiplicity of characters selected always either imposes enormous numerical demands on population size or causes a weakened selection for individual characters. One simply cannot have many characters *and* intense selection for each. The top line of *(a)* in *Figure 7* shows that, selecting at 10% for 10 characters, would demand no fewer than 10^{10} plants for an expectation of one resulting variety. This sort of level of operation is of course impossible for any plant breeding programme and yet the objective is superficially reasonable: a 10% selection rate is quite weak and 10 characters selected for is a common enough situation. The next two lines of the *Figure* show the effect on numbers of relaxing selection and reducing the characters, the two practical compromises available to the plant breeder.

MULTIPLE SELECTION

(a) The demands of numbers

Suppose: N plants, p selection rate, n characters and one selection resulting

$$N = \left(\frac{1}{p}\right)^n$$

N	p%	n	i	R
10^{10}	10	10	1·8	12·6
10^3	50	10	0·8	5·6
10^2	1	1	2·7	18·9

i selection intensity, h^2 heritability

$R = ih\sigma$ = expected genetic advance for rubber yields, $h\sigma \simeq 7$ lb

(b) A selection index

$$H = b_1 x_1 + b_2 x_2 + b_3 x_3 \cdots$$

(c) An economic selection equation in sugarcane

Cane yield Y, sugar percent Q, profitability P

$$P = a + bY(Q - 5)$$

Figure 7. Aspects of multiple selection in plant breeding.

The last two columns of *(a)* in *Figure 7* illustrate numerically the effect of varying the selection rate. Using data of ROSS AND BROOKSON (1966), the expected genetic advance in rubber yields (pounds per tree per year) can be very roughly calculated. Weak selection greatly reduces the response.

The moral, then, is that the plant breeder must minimise the number of characters if he wishes to maintain a high rate of progress for major characters; alternatively, if many characters must be accepted, then one must expect poorer progress as an inevitable statistical result. In general, a breeding programme needs a set of priorities, carefully defined in terms of the inevitable compromises and the practical possibilities of the situation.

Implicit in the foregoing discussion is the assumption that the characters selected for are independent. In this case successive selection, character by character, would be acceptable. Often, however, characters are correlated and, if negatively so, then successive (or tandem) selection will fail; instead, it is necessary to select simultaneously for both characters, aiming at an acceptable compromise. In general, simultaneous selection is always as efficient as successive selection and much *more* efficient when there are negative correlations. Ideally, one would always use a selection index *[(b)* in *Figure 7]* which is constructed to allow for heritabilities and correlations; in practice, the genetic information is rarely available, the computing has (until recently) been prohibitively heavy and the gain in efficiency may not outweigh the labour of getting the necessary measurements. Nevertheless, the *principle* of simultaneous selection remains important.

A different aspect of simultaneous selection is referred to at *(c)* in *Figure 7*. We may desire to weight characters according to economic value. No problem arises if the characters are economically independent but they may not be, in which case we require an expression that estimates value in terms of the levels of expression of the characters. The example concerns sugar-cane and the economic selection equation relates profitability to a compound of cane yield and sugar content. The equation says, in effect, that the latter is the more important character.

CONCLUSIONS

Finally, I will try to summarise my thesis in the form of a short statement of what one might call a breeding philosophy. The aim of a plant breeding programme is to maximise genetic advance, both now and later. For this, we need the following:

(1) a wide genetic base, systematically supplemented;
(2) large populations and maximal genetic recombination;
(3) breeding plans which are rationally founded on an understanding of history of the crop and on genetic analysis of its economic characters;
(4) simple or simplified selection procedures (which will often be based on correlations);
(5) polygenic rather than oligogenic disease resistances whenever possible;
(6) understanding of the role of heterozygosity and heterogeneity in our producing populations; and
(7) optimal multiple selection procedures arrived at by a combination of operational, genetic and economic analysis.

REFERENCES

*ALLARD, R.W. (1960) *Principles of Plant Breeding*. New York: John Wiley & Sons, Inc.

*ALLARD, R.W. AND BRADSHAW, A.D. (1964) Implications of genotype-environmental interactions in applied plant breeding. *Crop Sci.*, **4(5)**, 503.

*FALCONER, D.S. (1960) *Introduction to Quantitative Genetics*. Edinburgh: Oliver and Boyd, Ltd.

GILBERT, N.E. (1961) Correlations in plant breeding. *Euphytica*, **10(2)**, 205.

GILBERT, N.E. (1967) Additive combining abilities fitted to plant breeding data. *Biometrics*, **23(1)**, 45.

ROSS, J.M. AND BROOKSON, C.W. (1966) Progress of breeding investigations with *Hevea brasiliensis* III. Further data on the crosses made in the years 1937–41. *J. Rubb. Res. Inst. Malaya*, **19(3)**, 158.

*SIMMONDS, N.W. (1962) Variability in crop plants, its use and conservation. *Biol. Rev.*, **37(3)**, 422.

*SPRAGUE, G.F. (1966) Quantitative genetics in plant improvement. *Symposium on Plant Breedings*, 315. Ames: Iowa State University Press.

STEVENS, N.E. (1948) Disease damage in clonal and self-pollinated crops. *J. Am. Soc. Agron.*, **40(9)**, 841.

SUNESON, C.A. (1960) Genetic diversity—a protection against plant diseases and insects. *Agron. J.*, **52(6)**, 319.

VAN DER PLANK, J.E. (1963) *Plant Diseases: Epidemics and Control.* New York: Academic Press, Inc.

*WALKER, J.T. (1968) Selection and quantitative characters in field crops. *Biol. Rev.*, **(in press).**

*Not specifically cited in the text.