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Methods of Production of New Varieties [and Discussion]

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Methods of production of new varieties

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A review is given of the methods in general use in the breeding of crops belonging to the major groups of crop plants and an assessment is given of the important factors that determine their efficiency, especially gene–environment interaction in the early segregating generations. Variations of the standard techniques including generating homozygotes through single seed descent, cytological production of homozygous diploids, multiplication of advanced segregating bulk populations without selection, and the production of F_1 hybrid varieties in inbreeding crops, are outlined and assessed. The importance of production-scale testing to supplement data from plot trials, and its relevance to the organization of plant breeding and to the successful identification of superior selections, are considered.

It is now well understood that the prime determinant of the methods practised in plant breeding, as distinct from techniques for the induction of agronomically useful variations, is the crop's breeding system. Consideration of breeding systems focuses on the lineal relationship between the gametes at reproduction and their control of the genetic structure of populations. Of the major world crops, three of the five major cereals and most of the important oil and protein crops, including cotton, soybean and the pulses, accounting for two-thirds of the world's food, are inbreeders. Among naturally outbreeding crops, maize is pre-eminent, contributing 20% of annual grain supplies and a substantial amount of forage production; others include sunflower and many forage grasses and forage legumes. Clonal crops such as the orchard and soft fruits, sugar cane and the potato are also outbreeders in which sexual reproduction is bypassed by natural or managed methods of vegetative reproduction.

PURE-LINE VARIETIES

The genetic improvement of most inbreeding crop plants is commonly operated through the development of homozygous lines automatically generated by automatic self-pollination according to routine methods of pedigree selection (Bingham 1975). This method owes its worldwide success to a few very simple, decisive factors: it is simple to understand and operate and has been widely applied even where a minimal level of support technology is available; selection of one parent is invariably predetermined by the genotypic uniqueness of the best modern varieties while the other is selected on the basis of complementing characters or on the results of diallel test crosses; the system is self-propelling, generating improved parents for subsequent hybridizations and therefore guaranteeing stepwise improvement of performance without requiring astronomically large segregating populations and, given reasonable control of mutational changes and of outcrossing during multiplication, a stable agronomic performance of selections is guaranteed.

In common with several other routine methods of plant breeding, pedigree selection is a long process from when parents are hybridized to the release of a new variety; it is therefore less responsive to constantly changing objectives than rates of change in agricultural technology frequently demand. To overcome this limitation, winter nurseries in the Southern Hemisphere, enabling two generations of selection each year up to F_5 or F_6, are now in common use, thus reducing the timescale of selection by about 25 %.

The most recalcitrant problem of pedigree selection is the failure to identify genotypic values of individuals in early generations when gene–environment interactions cannot be identified, and selection decisions on economic characters like grain yield are largely an act of faith. Although significant correlations exist between performance in the early and later generations (Lupton & Whitehouse 1957; De Pauw & Shebeski 1973), the likelihood of identifying extreme genotypes in the early generations equates with random selection (Knott & Kumar 1975), which explains the irreducible level of uncertainty that still surrounds plant breeding programmes.

Variations of the pedigree selection method

Variations of the pedigree selection method have been proposed to reduce environmental effects during early selection. One of the best known involves the manipulation of the generations as bulks until F_6–F_8, subject only to natural selection and the elimination of the obviously unacceptable segregates, thus ensuring maximal retention of recombinants before selection begins. The advantage of the method as compared with low selection intensity of single plants in F_2 or F_3 is marginal, since the inevitable ear/row selections from bulks are subject to the same cryptic environmental interactions as are selections during early generations. There may be some improvement in the reliability of selecting in later generations from bulks, since homozygosity will ensure greater correspondence between genotypic and phenotypic values, but the increase in precision of selection cannot be expected to be of a very high order.

Bulk multiplication of segregating generations has also been advocated for subjecting poorly adapted genotypes to natural selection before screening for agronomic characters. Except that high density plantings allow inter-plant competition and favour aggressive genotypes, it is not clear why similar pressures do not operate in standard pedigree selection. Furthermore, natural selection and breeding objectives are seldom co-directional for economic characters, and genotypes with unacceptable expressions for characters such as tiller and seed number are liable to differential multiplication under natural selection, while others specified as important breeding objectives would be reduced or even eliminated.

It is not possible to report precisely on the use of bulk methods. It appears that the systems commonly applied are a modification of the original scheme whereby selection is postponed only during F_2 and F_3 when genotypic values are most uncertain.

Another modification of pedigree selection that is receiving attention is that known as single seed descent (see also Jinks, this symposium). In this, individual lines up to F_6 or F_8 are successively derived through a single, unselected seed saved in each generation. Large populations are grown under controlled conditions to promote reduced generation time, and homozygosis is achieved quickly, before selection commences, giving the advantage of improved correspondence of genotype and phenotype expected from delayed selection on bulk populations.

The probability of retaining the best genotypes through single seed descent equals that in pedigree selection (Knott & Kumar 1975), while theoretically it appears to allow prediction in

F_2 of the potential range of variation, thus enabling reliable culling at an early stage (Jinks & Pooni 1976). In common with the bulking of the early generations, single seed descent only partly eliminates uncertainties due to gene–environment interactions, and the method neither reduces the timescale nor the extent of field selection. Its use will necessarily be confined strictly to annual crops and its general value will depend entirely on possible advantages in retaining superior recombinants until environmental effects can be better assessed.

Another possible refinement of pedigree selection is the isolation of haploids from F_1 hybrids for the single-step creation of homozygous diploids. Two techniques are being investigated: the culture of haploid microspores (Sunderland 1978) and the formation of haploids after differential chromosome loss in progeny of F_1 hybrids. The culture of microspores has been claimed to have been successful in *Nicotiana tabaccum*, while only the cross between hybrids of *Hordeum vulgare* and *H. bulbosum* are being exploited to give haploids through chromosome loss in the F_1. Although programmes using these techniques are now established, they are still in the experimental phase, and their adaptation for routine breeding, while appearing not particularly promising, cannot yet be confidently assessed.

The importance of gene-environment interactions

Gene–environment interactions are, of course, not confined to the early segregating generations: they intrude universally throughout all programmes. Analysis of interactions indicate that although site effects are important, the larger and most refractory interactions are invariably associated with seasons. Site interactions can be minimized by careful selection of sites and by good trials management, whereas seasonal effects are unpredictable and irreducible. Thus plant breeders have no option but to select for stable performances over several seasons and therefore the long operational timescales associated with standard breeding methods are not without advantages in eliminating types that are excessively sensitive to seasonal effects.

Site interactions raise other issues, and while they are consistently smaller than seasonal effects, it is doubtful whether they are given adequate consideration in planning breeding programmes. In the famous experiments of Finlay & Wilkinson (1963), mean yields showed that, while the range in environmental sensitivity was wide, varieties with greatest stability also had highest mean yields. This pattern, however, does not exclude specific interactions leading to superior local adaptations. Extensive data from national trials by the National Institute of Agricultural Botany, Cambridge, and from the worldwide wheat variety trials conducted by the University of Nebraska indicate that site interactions are not common except across relatively very wide geographical areas. Some narrower regional adaptations are, however, indisputable. In the U.K., for example, different varieties have to be recommended for the west of England, especially to provide different patterns of disease resistance, and commonly for Scotland, where temperature differences are important. The relatively low frequency of site interactions may, however, be partly a reflection of their elimination during selection rather than a true indicator of the absence of regional adaptation: genotypes with significant interactions are likely to be discarded early during a breeding programme, whereas those exhibiting homoeostasis over sites are retained. Such influences can be minimized only by early testing at many sites and ensuring the selection of stable, contrasting patterns of adaptation, before entry into national trials.

F_1 HYBRID VARIETIES

Improvement in outbreeding species has been dominated by the highly successful programme on hybrid maize in the United States (Sprague & Eberhart 1977). The value of F_1 hybrid varieties and suitable methods for hybrid seed production had become clear in maize by 1920, and currently grain production based on hybrids predominates in every major maize-growing area of the world. Furthermore, the methodology for producing hybrid maize varieties has been applied with only minor modifications to most major outbreeding crops which allow pollination control. The crop species in which F_1 hybrids are in general use include several ornamentals, many vegetables, particularly the *Brassica* crops, onions and to a lesser extent carrots, sugar beet, and two major cereals, sorghum and maize. It is now accepted that the economic advantages of hybrids are not confined to yield alone but are also due to the impressive level of crop and product uniformity, which are invaluable features of F_1 varieties.

Outbreeding crops

The hybrid varieties initially developed in maize were genetically heterogeneous populations derived from four inbred lines, the so-called double-cross hybrids. These were a compromise between maximizing heterozygosity and the constraints on cost of hybrid seed. The greater yield and uniformity of homogeneously heterozygous hybrids based on two inbreds have only been exploited recently after the development of inbred lines capable of satisfactory seed production in single-cross hybrids. Currently, most F_1 hybrid varieties in use in the U.S.A. are single-crosses.

Following the discovery of the nucleo-cytoplasmic system of male sterility, male-sterile inbred lines whose fertility could be restored by complementary alleles completely replaced monoecious inbreds in the production of commercial F_1 seed. The superiority of the T (Texas) cytoplasm in maximizing male-sterility and in promoting high fertility restoration with appropriate restorer alleles, and its minimal pleiotropic effects on production characters, resulted in its almost universal use in female inbreds until 1970, when lines carrying this cytoplasm proved to be highly susceptible to southern corn blight and had to be discontinued. Since then a satisfactory replacement has not been developed and hybrid maize is once more being produced from mechanically detasselled, monoecious lines. This, however, must be considered to be only a temporary reversal in the genetical control of hybrid seed production in the crop.

Inbreds possessing superior combining ability are selected according to one of several well established methods. Genotypes that possess above-average combining ability can be identified during early generations of inbreeding, and since specific and general combining ability are highly correlated, initial screening is for high levels of general combining ability by using testers with a broad genetic base such as varieties ('top' crosses) or double-cross hybrids. Promising selections based on the initial test crosses are further mated to inbred testers for detecting specific combining ability in pairs of lines for commercial hybrid seed production.

GENETIC DIVERSITY AND THE ISOLATION OF COMPLEMENTARY INBREDS

Undoubtedly one of the most consistent conclusions that has emerged from the well documented hybrid maize programmes is the importance of maximizing genetic diversity between the source populations from which inbred lines are derived. The superior hybrids of the early period in the development of hybrid maize owed their success to the diversity inherent in the historical introgression of Southern Dent and Northern Eastern Flint genotypes. More recently, the same principle has emerged from hybrid maize programmes in the tropics, where production has been dramatically advanced after identification of superior combining abilities in inbreds derived from one dent and three unrelated flint populations. Inbred lines derived from these diverse stocks have generated hybrids with outstanding agronomic performances, which have quickly replaced the existing non-hybrid varieties adapted to tropical regions (Wellhausen 1978).

It has also become clear that superior inbreds can only be established after intense selection for agronomic characters, as well as rigorous screening for combining ability for grain yield. It is not surprising, given the decisive role of the source of origin of the base populations and the unpredictability of complementarity for yield between genotypes, that the frequency of isolation of superior inbred lines has been universally of the low order of less than 0.1 % of the total number studied. Clearly, the derivation of inbred lines for the production of F_1 hybrids cannot be regarded as a short-cut to success in plant breeding.

Continuing improvement of inbred lines

An obvious method to advance hybrid performance is through the recovery of improved inbreds from among selfed progeny of the best hybrids. The method is essentially pedigree selection and is applicable to outbreeding species only if self-incompatibility mechanisms do not prevent or seriously restrict inbreeding. Recombination among inbreds derived from superior F_1 hybrids allows further accumulation of alleles favourable for heterosis and second-cycle inbreds derived in this way are now in general use in commercial hybrids used in the United States. It is significant that, over the past 50 years, the ratio of the yield of inbreds to hybrids has remained stable at slightly below 0.5 (D. N. Duvick, personal communication). Thus, cycles of reselection for favourable alleles for yield improvement have failed to raise the yield of inbreds relative to hybrids, in spite of evidence for the overwhelming importance of dominance and of additive gene action in controlling yield expression.

Population improvement

The genetic constitution of the base material determines success in selection for combining ability, and its importance is reflected in extensive searches for the most efficient methods for upgrading the genetic status of populations. The objective of population improvement is simply to increase the frequency of favourable alleles before the isolation of inbred lines, and thus increase the probability of detecting superior genotypes. The methods used, which comprise both mass selection and various forms of progeny testing, are routines of varying levels of precision for accumulating alleles through recurrent selection over generations. While reflecting flexibility in respect of detail, all are designed for stepwise advances from base populations and, concurrently, to allow the production of interim hybrids, thereby reducing the time required for initial commercial exploitation. The average gain per cycle achieved by the different methods on a great range of material indicates that they are all almost equally effective, and the case for elaborate progeny tests has not been established.

Among several systems of recurrent selection, of special interest is selection within families replicated at several locations to minimize gene–environment interaction and the reconstitution of advanced generations from parents with high scores over several sites (Longquist 1964).

Reciprocal recurrent selection designed to improve the success of interpopulation crosses operates on two base populations. Reciprocal crosses, which form the basis of each selection cycle, involve tests for combining ability by using heterozygous or inbred testers from each population in combinations with selected genotypes from the other. Phenotypic selection within the two populations increases the frequency of favourable alleles for agronomic performance, while the use of progeny tests increases the probability of selecting inbreds with improved general and specific, interpopulation combining ability. A full summary of the impressive gains due to reciprocal recurrent selection for improvement in the performance of interpopulation crosses is given by Sprague & Eberhart (1977).

Incompatibility mechanisms and hybrid varieties

The development of hybrid varieties is feasible only where simple procedures for mechanical pollination control is possible as in monoecious maize, or where nucleo-cytoplasmic systems of control of male sterility allow large-scale production from male steriles as in maize, sorghum, sugar beet, onions and carrot. Exceptionally, as in *Brassica oleracea* (Thompson 1964), specialized control by the sporophytically controlled incompatibility mechanism has also been elegantly exploited.

Hybrid varieties in inbreeding crops

Of the crops that are predominantly inbreeding, the tomato is unique in that costs of hand emasculation and pollination for the production of F_1 varieties can be borne by charges on hybrid seed: in northern Europe, glasshouse tomato production is now based almost exclusively on hybrid varieties. Their success was not to be expected, since the level of heterosis recorded experimentally in the tomato has been minimal (Williams & Gilbert 1958), and pure-line varieties seemed to offer several advantages. It now seems probable that the greater opportunity for assessing gene–environment interactions in F_1 hybrids, which allow adequate replication in the first (and only) generation, may account for the undoubted success of F_1 hybrid tomatoes. Failure to identify reliable selections in F_2 and F_3 due to exceptionally large environmental interactions is probably even more important in fresh fruits and vegetables than in most other crops.

Although worldwide interest in F_1 hybrid cereals emerged after the discovery of nucleo-cytoplasmic control of sterility in the Triticineae, the exploitation of hybrid cereals has so far not proceeded generally beyond the research phase (Sage 1976; Hughes & Bodden 1978). A few hybrid varieties of barley, in which elimination of gametes containing the male fertile alleles is controlled by tertiary trisomy have, however, been developed to a commercial stage (Ramage 1965). Mutations (*ge*) closely linked to the male-fertile, *Ms*, allele, which cause the elimination of the male gametes (*Msge*), formed by male-fertile genotypes $\left(\frac{Msge}{msGe}\right)$ are also being studied for the development of hybrid barley (Foster *et al.* 1979). These genotypes are non-restorers of male fertility and are essential for large-scale multiplication of $\left(\frac{msGe}{msGe}\right)$ male-sterile lines for commercial seed production. The use of nucleo-cytoplasmic male sterility has recently also become possible for the development of hybrid barley following the discovery of sterile and restorer genotypes in *Hordeum spontaneum* (C. A. Foster, personal communication).

A continuing advance and the imminent release of hybrid varieties of wheat by using nucleo-cytoplasmic sterility is being claimed by seed companies in the U.S.A., but a similar programme at the Plant Breeding Institute, Cambridge, has been discontinued.

Apart from evidence that heterosis in inbreeding cereals is not large and that it can be fixed in pure lines, the restructuring of near autogamous floral mechanisms for open pollination is a major problem. Furthermore, most nucleo-cytoplasmic systems, even those extensively studied in maize, give only patchy fertility restoration in hybrids, which reinforces doubts on the potential of hybrid cereals for the near future. It may be noted, however, that F_1 hybrid seed produced by hand emasculation is reported to be developed in cotton in India where labour costs are presently not limiting, but the scale of the operation is unknown (Davies 1979).

Synthetic varieties

Outbreeding species that do not offer satisfactory mechanical or biological methods for developing F_1 hybrids are improved by selection of foundation genotypes for the establishment of genetically closed (isolated), open pollinating populations. Crops improved by these methods include self-incompatible forage grasses and legumes and many outbreeding vegetables. The methods do not differ significantly from population improvement and the derivation of inbreds already described, and comprise phenotypic recurrent selection as in forage grasses (Breese & Hayward 1972), or recurrent selection for combining ability based on progeny tests.

Tests for combining ability, where applied to the selection of foundation genotypes, concentrate on general combining ability by using heterogeneous testers, or, when the number of lines have been reduced to manageable numbers, polycross tests; specific combining ability between pairs of genotypes is of less importance for these varieties. The choice of whether inbred lines, heterozygous family lines or heterozygous clones are used as foundation genotypes rests on the ease of imposing inbreeding and on the vigour of inbreds in a given species. Since many outbreeding species are relatively self-incompatible, restricting the use of inbreds, heterozygous genotypes increased clonally for initial seed multiplication frequently replace sexual lines as foundation stocks.

Since synthetic varieties are maintained as closed populations during several generations of seed multiplication before commercial use, a major problem is the balance between maximizing response to selection and the prevention of loss of vigour through inbreeding, which will negate the responses. Estimates based on experimental data in maize (Kinman & Sprague 1954) indicate that six is the optimum number of unrelated foundation genotypes for maximizing advance under selection without incurring substantial reduction in vigour from inbreeding in synthetic varieties. One suspects, however, that in practice the number used is considerably greater.

Clonally propagated crops

Many crops, including citrus, most temperate orchard fruits (apples, pears, peaches and cherries), the potato, sugar cane and even some tropical forage grasses, are propagated vegetatively. In these, commercial varieties are heterozygous genotypes in which all the units of production form a genetically uniform clone except for variation due to accumulated mutations in somatic cells protected from selection. Indeed, the commercial exploitation of such spontaneous, somatic mutations has played an important role in the improvement of crops in this group.

For obvious reasons, vegetatively propagated crops are cultivated for their fruits, roots, tubers, stems or leaves, and seedlessness is frequently an additional virtue. With a few exceptions, clonal crops are outbreeders in which, *ipso facto*, production units are single heterozygotes selected from among heterogeneous family progenies. Furthermore, since many are fresh food crops, varietal specification must conform very precisely over a range of characters, while methods of breeding reflect the fundamentally different biological and commercial specifications of the various species within the group.

Selection routines in the potato

The general principles applicable to crops, which are naturally propagated vegetatively as distinct from those in which vegetative systems are imposed, e.g. apples or cherries, can be illustrated by reference to an example taken from potato breeding (Howard *et al.* 1977).

Choice of parents for hybridization was by reference to the best currently established varieties possessing complementary characters. The range of variation expressed in F_1 progeny, among which selection is practised, is particularly difficult to predict in this group of crops, and test crosses involving modest numbers of segregates are commonly studied initially to provide a guide to the total numbers required to allow a reasonable chance of recovering suitable segregates. Unpromising crosses are eliminated after preliminary test crosses, while others are repeated on a larger scale. Because of the number of character specifications that must be met through selection and of the heterozygous nature of the parents, very large progeny numbers are essential (Williams 1959).

The total number of progeny seedlings studied in the potato family cited here totalled 17582, which is average for current potato breeding programmes: examples of progeny numbers exceeding this by a wide margin are, however, common. Following elimination first of seedlings in the F_1, and at later stages of clones, on the basis of minimal criteria for seven economic characters, on general agronomic performance and on the basis of preliminary yield trials, six clones (*ca.* 0.035 % of the initial segregating population) survived for inclusion in national trials. This very modest recovery rate will almost certainly have been reduced further, probably to no more than 1 in 17000, when the results of national trials have been completed.

Intensity of selection in this programme was uniform and relatively weak over the ten clonal and one seedling generations: only segregates with obviously unacceptable environmental interactions were eliminated in any one season. As with most potato breeding programmes, selection was practised on a single site that could favour specific site interactions and lead to unsatisfactory performance in national trials where high average performance over many sites is sought. Studies on variety–site interactions in the potato have shown that major varieties such as King Edward, Maris Piper, Désirée and Pentland Crown, all show significant adaptation to certain production regions in England, indicating that site interactions should be considered in the organization of potato breeding programmes in this country.

Selection in tree crops

A number of clonally propagated crops, especially tree species, present unique problems in breeding methodology. After germination, seedlings enter a juvenile phase which may persist for several years, during which plants lack physiological competence to flower, and selection for fruit characters cannot commence. Even selection for vegetative characters such as tree form, leaf production, bud dormancy and disease resistance cannot be practised with confidence because of the general morphogenetic differences that are associated with juvenility. A reduction in juvenility is possible in some species by propagating seedlings on special root stocks, but the additional routine of handling large numbers of unselected seedlings involves substantial extra time and expense.

Since natural systems of vegetative reproduction are absent in most tree crops, selected genotypes for replicated orchard trials have to be propagated on suitable stocks. The number of years required for several cycles of vegetative reproduction places further serious limitations on the operation of plant breeding in this group, which is reflected in the overall modest success recorded in the production of much-needed new varieties in several of the crops.

The organization of plant breeding

Plant breeding in many countries is shared between private companies and government institutions. In the U.K., government institutions, notably institutes of the Agricultural Research Council and of the Departments of Agriculture, have historically played a predominant role both in variety production and in research support. Where cost/benefit ratios have been estimated (Simmonds 1974), investment in plant breeding has shown favourable returns and the involvement of private companies has increased in the U.K. during recent years since the provision of legal protection of new varieties in 1964. Currently, the size of breeding programmes in the public and private sector is judged to be approximately equal. In other countries in the European Economic Community, private companies have always played major roles in variety production, with government institutions supplying research support. This, too, is now the position in the U.S.A., where large, internationally based seed companies have become dominant in practical plant breeding.

Worldwide experience has shown that, while operational success in variety production is not a monopoly of either the public or the private sector and that adequate research support is essential for the success of both sectors, the range and complexity of problems currently associated with intensive production systems are on a scale that is new to agricultural research. Of these, the vulnerability of the major crops after erosion of nuclear and cytoplasmic variability, and the ecological imbalance created between crops and their diseases, are only the most obvious areas of concern requiring medium-term, if not long-term, perspectives in research.

Whereas the private sector will continue to depend for research support in plant breeding on the resources of the Government research services, it is clear that private breeders are frequently well placed to assess the economic worth of new selections. Many private organizations are engaged in commercial farming or horticulture on a large scale and are able to assess the behaviour of new varieties at production levels. Many crucial factors, which are difficult to quantify experimentally and which often become apparent only on a 'field' scale, can then be assessed. This is particularly relevant to crops for which adequate trial systems have not been available, and in this country it is the glasshouse, fruit and vegetable crops that have been least adequately served in this respect. It is vital, for success from investment in plant breeding, to appreciate the importance of limiting factors imposed during production and marketing, which intervene after the packets of breeder's seed have been sealed. When these practical requirements are ignored, even the most infallible genetical methodology at nursery levels will be largely wasted.

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Discussion

D. R. Knott (*Crop Science Department, University of Saskatchewan, Saskatoon, Canada*). I wondered why Professor Williams indicated that lines developed by the single seed descent procedure should be carried to the F_8 or F_9. Adding several extra generations would reduce one of the main advantages of the single seed descent procedure, the reduction in the time required to produce a new cultivar.

W. Williams. One of the advantages of single seed descent is the achievement of homozygosity before selection, giving a better correspondence between genotype and phenotype. Selection in earlier generations could of course be practised, but this would reduce some of the value of single seed descent and such earlier selection would not give a timescale shorter than pedigree selection.