Z. Pflanzenzüchtg. **89**, 1—18 (1982)

ISSN 0044-3298 / InterCode: ZEPZAD

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A Synoptic Study of the Methods and Categories of Plant Breeding¹)

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With 2 figures and 3 tables

Received March 17, 1982 / Accepted March 19, 1982

Abstract

The general methodology of plant breeding is examined with regard to a number of topics, viz. classification in categories; comparing operative processes; quantitative variability utilized; enhancing efficiency of selection; possible help from quantitative genetics.

Breeding methods are classified according to the propagational type of resulting varieties into four "breeding categories", viz. line, population, hybrid, and clone breeding. Within methods three "breeding phases" are distinguished, viz. procuring initial variation, forming varietal parents, and testing experimental varieties. The total of quantitative variability that can be utilized in various phases of a breeding method is studied by analyzing the respective "varietal population", i. e. the hypothetical universe of all varieties of given type which at the start are expected to be producible. All breeding categories offer opportunities to benefit from the general advantage of selecting among parents instead of selecting in hierarchical or factorial systems of progenies of such parents. The most helpful quantitative-genetical tool seems to be the predicting of the response to one or more stages of selection, by which qualitative and quantitative alternatives within breeding categories can be compared as to efficiency.

Key words: Breeding methods — quantitative variability — response to selection — multistage selection — quantitative genetics

In the following, I plan to present a general discussion on the methods of plant breeding, focusing on the utilization of quantitative variability, and

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¹) Revised version of an invited paper read at the Fourth Meeting of the Section "Biometrics in Plant Breeding" of EUCARPIA, held at Poitiers, France, September 2—4, 1981.

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therein on such problems in which quantitative genetics may help the breeder to make his decisions.

If the creation of new varieties meeting the requirements of growers is the ultimate goal of every breeding program, it is likewise true that the success of such a program depends upon the choice of an efficient breeding method. Of course, the method of breeding is but one of the many factors of success. For instance, two factors of perhaps even greater importance than methods are the designation of a promising complex of objectives, including its flexible pursuing, and the selection of appropriate source materials to start from. These two kinds of decisions must for the most part be based on specific considerations which can hardly be discussed without reference to particular crops. The methods of breeding, too, are specific, but not so much to crops as to modes of reproduction and to types of variety to be bred. And besides, they all have the genetical fundament in common. For these reasons and others, breeding methodology is likely to form the central part of any general theory of plant breeding.

It is not merely the limited space available which here causes me to refrain from any attempt to treat breeding methodology in all its aspects. Rather, I shall intentionally confine myself to discussing a few methodological problems by means of a comparative view on the "categories of breeding" which I have used for classifying breeding methods in my teaching since 1963. In particular, I shall consider differences as well as analogies between these categories with respect to three main topics: operative processes of breeding; variability which can be utilized; enhancing efficiency of selection. Under each of these topics, methodologically relevant relations will be pointed out which are seldom if ever dealt with, and unpublished tools will be employed in investigating them. A look on the possible uses of quantitative genetics in plant breeding shall conclude the paper.

1. Defining and classifying breeding methods

Although arguing about terminology may not seem very fruitful indeed, I cannot dispense with giving a few introductory remarks on the issue of defining and classifying breeding methods.

Rather broad as well as more narrow meanings have been attached to the term "breeding method". I prefer to distinguish it not only from single "breeding steps" (for example: performing a test; making crosses) but also from "breeding techniques" (for example: inducing mutations; producing lines via haploids) which do not imply all the operations necessary for establishing a new variety. This is because I understand by a breeding method the total plan how to create a new variety or, in the special case of recurrent selection, an improved population for use as initial variation in another breeding program. Such a plan, comprising all the necessary breeding steps from the choice of source materials up to the final selection among experimental varieties, is clearly more than the sum of its parts. For, viewed singly, any breeding step is neither expedient nor inexpedient, but becomes useful only in the right place within a purposive method of breeding.

In planning a breeding program one has to decide not only on the particular steps to be performed in succession, but also on the quantitative dimensions of each of these operations. The assignation of proper dimensions to each step of a breeding program, being comparable to the problem of optimum allocation for a series of tests, may decisively contribute to the effectiveness of a method in practice. Notwithstanding one mostly characterizes breeding methods only qualitatively, i.e. by referring to kind and sequence of the operations involved.

Autors of textbooks and teachers, who are among the first to feel the need of classifying breeding methods according to some general principle, have done this by means of various criteria, which include: natural reproductive system; origination of initial variability; propagational category of resulting varieties.

The natural reproductive system which is required to make a certain method applicable seems to be that criterion which is most widely used so far (see for example: Baur 1921, Hayes et al. 1955, Poehlman 1979). It classifies the breeding methods into those for self-fertilizing, cross-fertilizing, and asexually reproduced crops. Grouping according to the origination of the initial variability to be utilized is mainly found in some German textbooks (see for example: Roemer and Rudorf 1941, Hoffmann et al. 1971). It leads to such classes as "breeding by selection" (which is the zero case, so to say, in which variability is on hand and therefore need not be produced), "breeding by crossing", "polyploidy breeding", and "mutation breeding". This principle of grouping suffers from several weaknesses which I discussed elsewhere (Schnell 1982).

In what follows I shall make use of the third criterion, propagational category of resulting varieties (Schnell 1969, 1978, Simmonds 1979). It emerged from an attempt to adapt the first-mentioned criterion, natural reproductive system, to the invention of hybrid breeding. This invention had added an artificial reproductive system, i.e. controlled crossing, which is practicable in both self-fertilizing and cross-fertilizing plants. And it had also become apparent that hybrid breeding requires special methods which are fundamentally different from the customary ones, whatever the mode of reproduction of the crop may be. If we then wish to use the type of variety to be bred for classifying breeding methods, the question arises how to differentiate those groups of varietal types which are relevant in this connection. It turns out that the last reproductive process taking place in the propagation of a variety can serve as the distinguishing feature, because it differentiates between, but not within, those categories. The four reproductive processes of propagation and the corresponding "propagational categories of variety" may be specified as follows:

1. Self-pollination with "lineal varieties", i.e. pure line varieties, multiline varieties, land varieties of self-fertilizing crops.
2. Panmictic cross-pollination with "population varieties", i.e. synthetic varieties, open-pollinated varieties.
3. Controlled crossing between seed and pollen parents (or some equivalent mechanism which prevents parental selfings or sibs from becoming part of the variety) with "hybrid varieties", i.e. single crosses, three-way crosses, double crosses, etc.
4. Vegetative propagation with "clonal varieties", i.e. clone varieties, land varieties of asexually reproduced crops.

When we classify breeding methods according to the propagational category of resulting varieties we get four "categories of breeding", which may be called "line breeding", "population breeding", "hybrid breeding", and "clone breeding".

Tab. 1 Four categories of breeding, and a set of queries differentiating between them

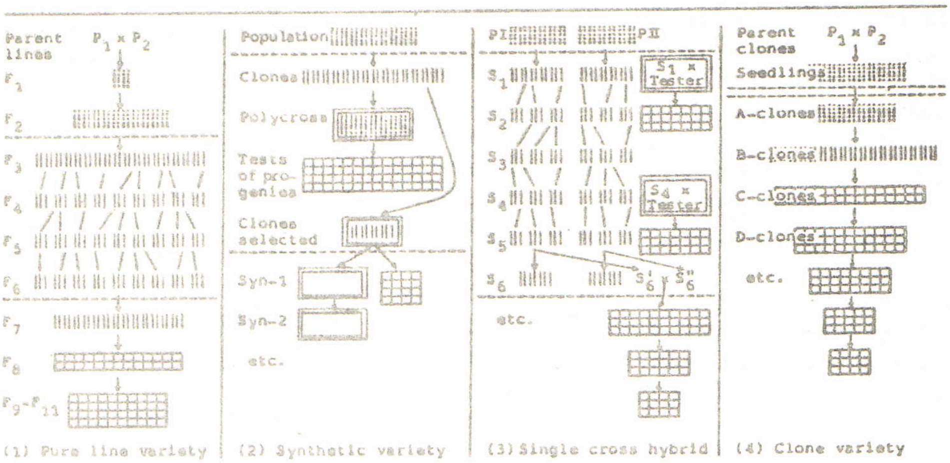
	Line breeding	Population breeding	Hybrid breeding	Clone breeding
Is heterosis a major yield factor in resulting varieties?	**no**	yes	yes	yes
Would varieties consisting of but one genotype be feasible?	yes	**no**	yes	yes
Can the plants of a variety be used for its own propagation?	yes	yes	**no**	yes
Are resulting varieties propagated by means of seeds?	yes	yes	yes	**no**

The system of breeding categories defined above may also be substantiated in the way of *Table 1*, wherein each category is shown to miss one characteristic which is common to the other three. The first row, for example, reminds us that heterosis is a major yield factor in all the categories except line breeding. By the way, because of the latter fact, it is unfortunate that terms like "heterosis breeding" are used synonymously for "hybrid breeding" by some.

2. Comparing operative processes of breeding

We now proceed to our first main topic, that is, to study and to compare the operative processes which are implied in the breeding methods of various categories.

In the interest of comparability I shall consider only "general" breeding methods, by which I mean methods being applicable under a wide range of conditions. Backcross breeding, for example, is to be regarded as a "special" method, because its utility is limited to gene transfer for the improvement of single traits with existing varieties. In this sense, then, the diagrams of ***Figure 1*** display the schemes of four general breeding methods, each of which belongs to a different category and is supposed to be more or less representative.



(1) Pure line variety | (2) Synthetic variety | (3) Single cross hybrid | (4) Clone variety

Fig. 1 Schemes of four breeding methods appropriate for indicated types of variety. For explanation see text

Scheme (1) refers to line breeding by means of the pedigree method, which is probably among the most popular methods of its category. Scheme (2) exemplifies population breeding, showing the development of a multiclone synthetic of a forage crop. Scheme (3) represents hybrid breeding for a single cross variety, starting with two populations, P I and P II, and providing for topcross tests of S_1-lines and S_4-lines as well. The final tests involve factorial crosses made between S_6'- and S_6''-lines which stem from P I and P II, respectively. Last, scheme (4) outlines clone breeding with an annual crop such as potato.

Taking a glance at the four schemes of *Figure 1* is sufficient to observe them to be formally different, but we want to study their operational differences, and to this end we have to look out for the operational analogies as well.

A useful tool which can help us compare the various breeding methods, is to divide them each into three distinct "breeding phases". These are to be defined in such a way as to comprise functionally different parts of the whole process of breeding. Referring to the envisaged functional contents, I shall designate the three breeding phases as follows:

1. Phase of procuring initial variation.
2. Phase of forming varietal parents.
3. Phase of testing experimental varieties.

In each diagram of *Figure 1* two dashed lines are drawn to separate the first phase from the second, and the second from the third, respectively. The second phase itself, however, is missing with scheme (4).

The breeding phases, although serving a definite functional purpose each, will now be seen to vary among schemes as to kind and length of the operative processes involved, and that in a manner which is largely characteristic of the respective breeding categories.

The first phase, procuring initial variation, is defined to include the necessary breeding steps from the choice of base materials up to the growing of those populations, or first segregating generations, from which the parents of the future varieties are to be taken or developed. As shown in diagrams (2) and (3), the initial variation for population and hybrid breeding is supplied by the respective base populations themselves. Hence, provided suitable populations are available, the year of growing them makes up the entire first phase. In schemes (1) and (4), however, the initial variation first arises with the F_2 and the seedling generation respectively, which, in turn, have to be produced from selected parents. We should note in this context that diagrams (1) and (4) are oversimplifications in that they both show but one cross. In practice, line as well as clone breeding starts from making many crosses simultaneously, the parents of which are chosen from base pools meeting the objectives. A wheat breeder, for example, might select forms with excellent yields and forms having high baking quality for use as P_1's and P_2's, respectively.

The second phase, forming varietal parents, consists in deriving and/or selecting those single plants, clones, populations, or lines, which are to become the immediate parents of the first generation of experimental varieties. Since in clone breeding the experimental varieties are established immediately from the seedlings, the second phase here vanishes. At the other extreme, in hybrid breeding this phase is longer than in any other category and would even require two more generations than are shown in diagram (3) if breeding were for three-way or double crosses. Hybrid breeding thereby becomes a kind of blind flight, because most of the selection must be done before one catches sight of any forms similar to the future experimental varieties. Particularly line breeding confronts the breeder with the choice of turning from the second to the third breeding phase earlier or later, therewith raising an important, though seldom discussed, methodological problem in practical breeding.

The third phase, testing experimental varieties, begins with the growing of the first generation of experimental varieties. This phase extends over more than one year in most cases, but forms nearly all the work in clone breeding. At the other extreme here stands population breeding, in which variety testing plays the least rôle, serving as a check of success rather than as a step of selection. This is because, in contrast to all other categories, mostly just one improved variety is built and tested. If the performance attained should not be satisfactory, a new cycle of breeding must be resorted to. Such breeding in successive cycles is the rule, of course, in the various methods of recurrent selection. A single cycle of any such method may operationally be viewed as a modified scheme (2) which is more or less condensed in the interest of a quick succession of cycles.

In passing I should point out that the term "breeding phase" is not to be confused with term like "varietal building phase" which are sometimes used for distinguishing the processes of creating new varieties from breeding processes intended for the improvement of base populations (WRIGHT 1974). In long-term breeding strategies proposed by various authors (e.g. SPRAGUE and EBERHART 1977, GALLAIS 1979, GEIGER 1982), population improvement by means of recurrent selection forms the central and continuous line of work. A variety building phase, i.e.: a program for the development of new varieties, may branch off from that line at each cycle.

3. Quantitative variability which can be utilized

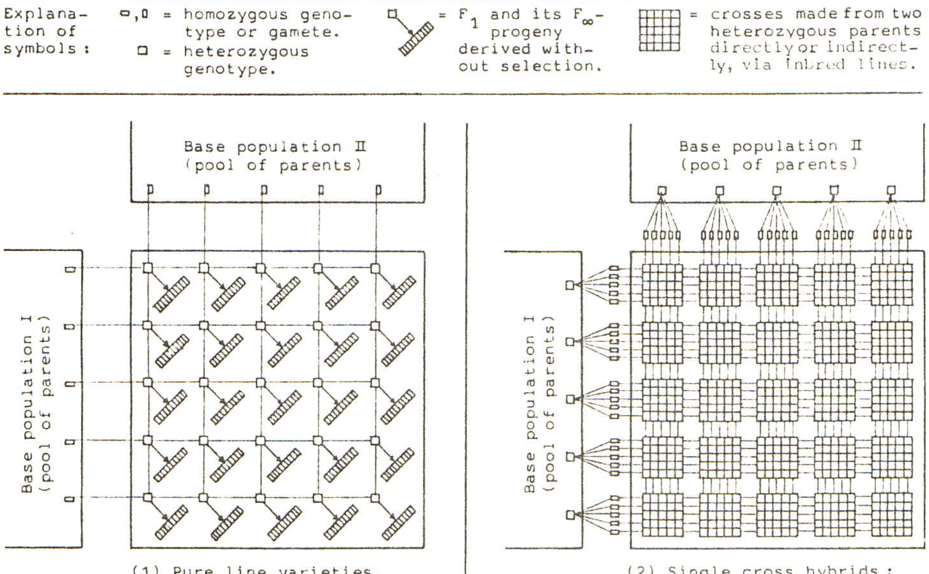
After comparing the categories of breeding as to some operational characteristics, we are going to consider analogies and differences between these categories with regard to quantitative variability and its utilization by selection in various breeding phases.

Most breeding methods provide several successive selection steps, which in part utilize different forms of variation. For example, at the start of a breeding program selection is among parents, but in the end selection is among experimental varieties. If we want to relate the various selection steps of a method to the total progress expected from selection, we must relate all these steps to a single basis of variation.

The tool I shall use for studying the total variation which can be utilized in a breeding program is to analyze the hypothetical universe of all the varieties of given type which at the start are expected to be producible. This hypothetical universe may be called the "varietal population". The idea of such a population is closely related to the recently developed concept of selection for "varietal ability" (WRIGHT 1974, GALLAIS 1979, GALLAIS and WRIGHT 1980). The varietal population applying to a given breeding program is determined by three things, viz. the base materials chosen, the type of variety to be bred, and the mating system which is implied in the breeding method adopted. Of course, a varietal population is open to biometrical description only when varieties are supposed to be replaced by measurements of some trait of performance, say yield.

Now I would like to investigate the varietal populations which apply to the four breeding methods depicted in *Figure 1*, but to simplify matters I shall restrict this for the present to the schemes (1), (3), and (4).

Figure 2 shows two diagrams, each of which pictures a varietal population and its parents. While the diagram on the left refers to line breeding, that one on the right happens to apply to hybrid breeding for single crosses just as well as to clone breeding. In the interest of comparability two base populations, or pools of parents, are assumed in either diagram. Strictly speaking this would be needed only in hybrid and clone breeding for the sake of securing a high level of heterosis in the varietal population. It is, however, not at all unusual to start line breeding by making a factorial series of wide crosses, the parents of which are taken from locally adapted forms on the one side and from remote forms having desired traits on the other.



(1) Pure line varieties, bred from single crosses

(2) Single cross hybrids ; clone varieties

Fig. 2 Diagrammatic representation of varietal populations resulting from the choice of two base populations in each case, for indicated types of variety. For explanation see text

The structure of the left-hand diagram of *Figure 2* is based on the assumption that orthogonal matings between the two pools of homozygous parents result in an infinite factorial of F_1's, each of which in turn gives rise to an F_∞-progeny. The factorial-like system of these hypothetical F_∞-progenies forms the varietal population in line breeding, supposing the initial variation of F_2's is to be produced from a sample of such F_1-crosses. The right-hand diagram, too, assumes that orthogonal matings between the two pools of parents result in an infinite factorial of crosses. But here the crosses themselves form the varietal population, and they come from heterozygous parents, from which they are made either directly or indirectly. The former applies to clone breeding, where each of these crosses represents the population of seedlings, or clones, produced directly from a pair of parents. In breeding for single cross hybrids, on the other hand, any such cross for its part is an infinite factorial of hypothetical single crosses produced by orthogonal matings between two arrays of unselected inbred lines. But each of these arrays of inbred lines traces back to one of the heterozygous parents (S_0-plants), so that the crosses may be visualized as being made from those parents indirectly.

The various successive selection steps during the course of a breeding program rapidly reduce the still producible part of the respective varietal population, only a tiny section of it being eventually produced for testing. It should also be mentioned that the initial sampling from the varietal population usually is by S_0-plants and lines in hybrid breeding, but is by crosses in line and clone breeding. Initial sampling, however, is likewise by crosses with HALLAUER's (1967) plan for the development of single cross hybrids from two-eared maize populations.

Tab. 2 Components of the genotypic variances of the varietal populations represented in *Figure 2*. For explanation see text

	Pure line varieties*)	Single cross hybrids; clone varieties**)
Between parental crosses	$\sigma^2_{.A'\infty} + \sigma^2_{.A''\infty}$	$(1/2)\sigma^2_{.A'} + (1/2)\sigma^2_{.A''} + (1/4)\sigma^2_{D}$
Within parental crosses	$\sigma^2_{.A\infty}$	$(1/2)\sigma^2_{.A'} + (1/2)\sigma^2_{.A''} + (3/4)\sigma^2_{D}$
Total between varieties	$\sigma^2_{.A'\infty} + \sigma^2_{.A''\infty} + \sigma^2_{.A\infty}$	$\sigma^2_{.A'} + \sigma^2_{.A''} + \sigma^2_{D}$

*) $\sigma^2_{.A'\infty} = \Sigma p'q'a^2$;
$\sigma^2_{.A''\infty} = \Sigma p''q''a^2$;
$\sigma^2_{.A\infty} = \Sigma(p'q'' + q'p'')a^2$.

**) $\sigma^2_{.A'} = \Sigma p'q'[a - (p'' - q'')d]^2$;
$\sigma^2_{.A''} = \Sigma p''q''[a - (p' - q')d]^2$;
$\sigma^2_{D} = 4\Sigma p'p''q'q''d^2$.

Proceeding to the biometrical description of the varietal populations pictured in *Figure 2*, I must here refrain from formularizing the means, however important they may be for the success of breeding. Formulae of the respective genotypic variances are given in *Table 2*, taking into account that each of these populations arise from two different base populations, but otherwise assuming the simplest genetical situation, i.e. no epistasis, no linkage, and equilibrium within and among loci in the base populations. Referring to the system of means of F_∞-progenies, $\sigma^2_{.A'\infty}$ and $\sigma^2_{.A''\infty}$ are the additive variances due to the genes originating from base populations I and II, respectively, while $\sigma^2_{.A\infty}$ is the average additive variance within F_∞-progenies. In the hybrid population, $\sigma^2_{.A'}$ and $\sigma^2_{.A''}$ are the additive variances due to the genes originating from base populations I and II, respectively, and σ^2_{D} is the dominance variance. The various component variances are specified in footnotes, adopting FALCONER's (1960) two-allele model with regard to all loci summed, i.e. writing *a* for half the phenotypic difference between the two homozygotes and *d* for the departure in phenotype of the heterozygote from the average of the two homozygotes. Further, *p'* and *p''* stand for the frequency of the more favourable allele in base populations I and II, respectively, with $(p' + q') = (p'' + q'') = 1$. The variances of the hybrid population were given in another form by ROBINSON et al. (1958) and, for less restrictive assumptions, by GRIFFING (1962), SCHNELL (1965), and STUBER and COCKERHAM (1966).

Staying for a moment with the footnotes, we observe the definitions of $\sigma^2_{.A'}$ and $\sigma^2_{.A''}$ reduce to those of $\sigma^2_{.A'\infty}$ and $\sigma^2_{.A''\infty}$, respectively, if the dominance deviation, d, vanishes, as it should be true with the F_∞-generation. The parallelism between these definitions on the left and right, which of course tells us nothing about the size of the variances in question, seems remarkable in so far as it is caused by the mere similarity of the respective varietal populations concerning their basically factorial structure. By the way, these definitions could also serve as a warning of the rather different things which might be involved when breeding research for example speaks of "additive variance" or "additive effects".

As regards the variances which can be utilized in various selection steps, *Table 2* shows how the genotypic variance, here labelled "total between varieties", is in each case composed of two parts, labelled "between parental crosses" and "within parental crosses". These two parts contain different component variances on the left side, i.e. in line breeding. On the right side, applying to hybrid as well as clone breeding, both parts contain the same three component variances, although in different proportions. The first and second of these components reflect the general combining ability (g.c.a.) of parents originating from base populations I and II, respectively, while the third is caused by the specific combining ability (s.c.a.) of pairs of parents. We should note that both line and clone breeding utilize the respective variances between and within parental crosses in different breeding phases, i.e. successively. Hybrid breeding, however, mostly utilizes these two variances simultaneously inasmuch as selection is practized within and among inbred lines. Another way of looking at this would be the statement that the two rows labelled "between parental crosses" and "total between varieties" give the variances among hybrids made from non-inbred and completely inbred parents, respectively (COCKERHAM 1956).

To illustrate the implications of the formulae given in *Table 2* by at least one specific example, we examine the way in which the two variances labelled between and within parental crosses are affected by the degree of genetic diversity between the two base populations chosen. Genetic diversity at individual loci is measured by the difference of gene frequency between the two populations, which in FALCONER's (1960) notation is symbolized by y, with $y = p' - p'' = q'' - q'$. Working from the respective expressions in *Table 2*, it is easy to show that the variance within parental crosses exceeds the variance between such crosses by the amount of $\Sigma y^2 a^2$ in line breeding, and by $(1/8)\Sigma(4p^2 - y^2)(4q^2 - y^2)d^2$ in hybrid or clone breeding, where $p = (p' + p'')/2$ and $q = (q' + q'')/2$. Thus, under our assumptions, the difference between the two variances vanishes in line breeding if $y = 0$ at all loci, but increases in favour of the variance within crosses if the genetic diversity between the two base populations is enhanced. As opposed to this, such enhancement of diversity diminishes the difference considered with hybrid and clone breeding, thereby increasing the relative significance of a careful selection among crosses prior to selecting within crosses.

Finally, regarding the rôle of the various kinds of genetic effects in different breeding categories, we may generalize the formulae of *Table 2* by saying that additive, dominance, and all sorts of epistatic effects can be utilized in full with clone breeding as well as with hybrid breeding for single crosses. Considerably lesser portions of these genetic effects are utilized in selecting among threeway and double cross hybrids (COCKERHAM 1961). Line breeding, on the other hand, can obviously capitalize only on such additive and epistatic effects as exist in the varietal population of F_∞-lines, so that dominance and dominance-like epistasis occurring in early generations cannot be utilized, and their action simply impedes selection.

To extend things to population breeding, we may assume that it starts from a base population which has been advanced by random mating from the hybrid population shown in *Figure 2* on the right. Then, the hypothetical infinite universe of all possible N-parent synthetics, which could be produced from the array of genotypes of the advanced generation used, forms the varietal population for this type of variety. The genotypic variance of the varietal population comes according to HILL (1971) approximately to

$$(1/N)\sigma^2_A + [(2N - 1)/4N^3]\sigma^2_D ,$$

where $\sigma^2_A = 2\Sigma pq[a - (p - q)d]^2$ and $\sigma^2_D = 4\Sigma p^2q^2d^2$. Thus, depending on the size of N, only a small portion of the additive effects and an even much smaller portion of the dominance effects can be utilized in breeding for synthetic varieties. Utilization of epistatic effects of all sorts also is incomparably less than in hybrid or clone breeding.

4. Ways of enhancing efficiency of selection

Turning now to selection, I shall first briefly review the factors determining the response to selection, which in the literature is also referred to as the gain from selection (see e.g. SCHNELL 1981), and later point to a class of opportunities of enhancing efficiency offered by the methods of breeding.

Let an array of genetic units (single plants, lines, or other groups of plants) be selected for their performances regarding some phenotypic value, x, in the hope to achieve an improvement in the retained fraction of units regarding the average outcome with respect to a genotypic value, y. The latter value may concern characters of the genetic units themselves and/or of genetically defined properties of these such as combining ability or other forms of varietal ability. Likewise the criterion of selection, x, may be a function of measurements gathered from the genetic units themselves and/or from some relatives, e.g. from progenies obtained by cloning, selfing, or crossing. In general then, this will be a process of indirect selection, even if x and y refer to the same trait. Suppose x and y are variables having a bivariate normal distribution, the expected response to such indirect selection, $R_{(y|x)}$, is well-known and may be written in the form,

$$R_{(y|x)} = i_x h_x r_{(G:x,y)} \sigma_y ,$$

where i_x represents the intensity of selection applied to x, h_x is the square root of the operative heritability of x, $r_{(G:x,y)}$ denotes the genotypic correlation between x and y, and σ_y symbolizes the standard deviation of y.

All four determinant factors shown on the right side of the above formula are open to the influencing control of the breeder. The intensity of selection, i_x, which is the selection differential expressed in standard units, depends on the dimensions given to the respective selection step, and that in a twofold but often conflicting way. For, this factor increases, although not linearly, when either the total number of entries under selection is enhanced or the number of entries to be selected is reduced. The second factor, h_x, comes the closer to its maximum, unity, the less the criterion of selection, x, is affected by environmental effects of all kind. Essential means for the control of such masking effects is not only a sufficient extent of testing, but also the use of appropriate experimental design, the application of optimum allocation, and therein, full regard to genotype-environmental interactions (SPRAGUE and FEDERER 1951, COMSTOCK and MOLL 1963). The third factor, $r_{(Gx,Gy)}$, calls for a high degree of relationship between the plants forming the criterion of selection and the genotypes which are to be improved as to genotypic value. Inasmuch as the latter genotypes are settled by the purpose the selection has to serve within the breeding program, an enhancement of $r_{(Gx,Gy)}$ can only be achieved by the choice of a better suited type of progeny for use as selection criterion. But sometimes $r_{(Gx,Gy)}$ can also be enhanced by putting the genetic units into a more favourable form before starting the selection process, for example by parental inbreeding. In this way one would at the same time achieve an improvement with regard to the fourth factor, σ_{Gy}, which otherwise is mainly influenced by the choice of the base materials to work with.

It must be mentioned that not infrequently the maximum response to selection can be attained by raising certain factors at the expense of others, since it is the product of all four factors which counts. Deducing the conditions for the maximum response is facilitated by the use of the above formula, in which the term h_x solely measures the correlation between the phenotypic and genotypic values of the selection criterion, but is not affected by the relation of x to y. Expressing things in this way also has the desirable consequence that all four categories of plant breeding get along with the same concept of "operative heritability" (STRUBE 1967), which is the broad sense heritability of an array of values or means arising of a given program of screening or testing.

Continuing with the response to selection, I wish to discuss another widespread opportunity of enhancing efficiency, that is, by selecting among parents instead of selecting in hierarchical or factorial systems of progenies of such parents.

Referring to *Figure 1*, we observe hierarchical systems of progenies occur in the second breeding phase with line and hybrid breeding, when in segregating generations selection is to be practized among and within lines. Factorial systems of progenies for example arise in the first breeding phase with line and clone breeding in case that all possible crosses should be made between two arrays of parents. If the two parental arrays crossed are identical, a diallel results, which may be regarded as a special case of a factorial system. In the varietal testing phase of hybrid breeding, too, factorial systems are met with, consisting here of single crosses or of hybrids of other type. Lastly, in breeding for synthetic varieties, N-factorial systems of crosses would be envisaged, although not produced, as varietal populations.

A simple tool for demonstrating the advantage of selection among parents over selection among their descendants consists in comparing the intensities of selection which are possible with an equal expense of testing in both cases. I will briefly report on such a comparison made between two possibilities of selecting among crosses for line breeding (SCHNELL and UTZ 1975). We aim here at selecting the cross being highest in varietal ability, $\bar{F}_\infty$, which means the expected genotypic value of all lines that can be derived from a given cross (called "line ability" by GALLAIS 1979). The two selection criteria to be compared are the midparent value, $\bar{P}$, and the cross mean, $\bar{F}_t$, determined in some early generation t, say in F_1 or F_2. Supposing limited capacity permits testing of N entries, which can be either parents or bulked crosses, selection would have to be practized among N cross means, $\bar{F}_t$, or alternatively among $M = N(N-1)/2$ midparent values, $\bar{P}$. By analogy with the formula given earlier we may write the ratio of the expected response to selection among the $\bar{P}$'s to that among the $\bar{F}_t$'s in the form,

$$\frac{R_{(\bar{F}_\infty|\bar{P})}}{R_{(\bar{F}_\infty|\bar{F}_t)}} = \frac{i_{(1.M)} b_{\bar{P}} r_{(G(\bar{P}).\bar{F}_\infty)}}{i_{(1.N)} b_{\bar{F}_t} r_{(G(\bar{F}_t).\bar{F}_\infty)}},$$

where $i_{(1.M)}$ and $i_{(1.N)}$ are the intensities of selection applying to the choice of the largest out of M and N predicted values, respectively. These two selection intensities and their ratio as well are listed in *Table 3* for a few selected values of N, assuming that the $\bar{P}$'s and $\bar{F}_t$'s are normally distributed. As seen from the Table, the ratio, $i_{(1.M)}/i_{(1.N)}$, increases with N, but at a quickly decreasing rate, staying close to 1.45 between $N = 12$ and $N = 48$. Thus, with such values

Tab. 3 Number of crosses for line breeding which are predictable from N tested entries, and resulting intensity of selection, for two criteria of selection and various sizes of N. For explanation see text

Number of entries tested	Number of crosses predictable from		Intensity of selection when selection is among		Ratio
	$\bar{P}$'s	$\bar{F}_t$'s	$\bar{P}$'s	$\bar{F}_t$'s	
N	$M = \frac{N(N-1)}{2}$	N	$i_{(1.M)}$	$i_{(1.N)}$	$\frac{i_{(1.M)}}{i_{(1.N)}}$
3	3	3	0.85	0.85	1.00
6	15	6	1.74	1.27	1.37
12	66	12	2.36	1.63	1.45
24	276	24	2.85	1.95	1.46
48	1128	48	3.25	2.23	1.46

of N, selection among midparent values would be superior to selection among cross means, as long as the ratio

$$h_{\overline{F1}} r_{(\overline{F1},\overline{F}_{\infty})} / h_{\bar{P}} r_{(\overline{G \cdot P},\overline{F}_{\infty})}$$

does not exceed the value of 1.45.

Similar advantages in favour of selection among parents exist with respect to the other factorial systems mentioned above. The advantages are largest, of course, with the N-factorial systems occurring hypothetically as varietal populations in population breeding, so that here selecting among parents only is the common practice. On the other hand, it mostly pays to restrict selection among parents to the first stage of a two-stage selection process, if selection among crosses utilizes additional genetic effects such as s.c.a. effects. This is why the hybrid breeder usually selects first among his inbred lines for g.c.a. and then among single crosses made from the better lines. With the hierarchical systems arising in segregating generations of line and hybrid breeding, too, it is apparently rewarding to select in a first stage among the heterozygous parents and in a second stage among sublines derived from the better parents (SCHNELL 1974, UTZ 1981, WEBER 1981).

5. Breeding methodology and quantitative genetics

When we finally come to look at those problems in which the plant breeder may be aided by quantitative genetics, we should realize that in planning and performing a breeding program one has to decide mainly on the following methodological points:

1. Category and type of variety to be bred.
2. Breeding method within category.
3. Dimensions of breeding steps within method.

As to the first point, hybrid varieties are now topical alternatives in many crops, and partially allogamous plants such as the field bean may even offer a choice of three categories, viz. line, population, and hybrid breeding. But the actual decisions on varietal category, and on varietal type within category as well, are reached on the grounds of given facts as to reproductive system, possibility of pollination control, epidemic pressure, general level of breeding and seed technology, requirements of the market, and other social and economic circumstances. Much less decisive would be any results gathered from genetic analyses of quantitative variability, except information on the relative amount of heterosis.

Secondly, regarding the choice among breeding methods within category, line breeding for example offers several named alternatives such as pedigree, single-seed-descent, bulk, F_2-progeny, and pedigree-trial method of breeding. These methods mainly differ with respect to the selection system provided for in the phase of forming varietal parents. The same is true with the numerous procedures proposed for population breeding, being distinct, apart from providing for pollination control or not, chiefly in their use of different systems of parental selection, which include mass, half-sib, full-sib, testcross, and

S_1 selection. As to the two other categories, we meet the contrastive situation that for clone breeding no qualitative alternative to the method outlined in scheme (4) of *Figure 1* seems to be known, whereas the scheme (3) given there for hybrid breeding is in practice never realized, at least not as a closed system like that. Rather, the main operations necessary for hybrid breeding such as improvement of base materials, development of inbred lines, producing and testing hybrids, are carried out in several separate programs each. These are planned individually and coordinated with great flexibility, thus requiring manifold methodological decisions. As the choice among alternative methods within any breeding category must be based on operational and genetical considerations as well, it may greatly profit from the general theory of quantitative genetics just as from specific studies in this field.

Thirdly, decisions on the dimensions of breeding steps within method are something like the daily bread for the breeder. For example, there is no performance test without allocation of plots, and no selection step without conscious or unconscious decision on the size of the fraction to be retained. Furthermore, the dimensions of successive breeding steps within the method adopted have to be brought into favourable proportions to each other. And wherever a breeder starts from several crosses simultaneously, as e.g. in line or clone breeding, he must determine the number of crosses and the size of progeny within crosses in consideration of the total expense possible. While hitherto such decisions on dimensions are mostly taken on the grounds of intuition and experience alone, they certainly could often be improved with the aid of quantitative genetics.

After all, it is the decision on breeding methods and their dimensions as well, i.e. choice among both qualitative and quantitative alternatives within breeding categories, which calls for helpful genetical and statistical tools. Quantitative genetics has developed various approaches for that purpose, which include: prediction of means and variances of varieties that can be built (e.g. BUSBICE 1970, HILL 1971); genetical formularization of the expected gain from selection (e.g. COCKERHAM 1961, GALLAIS 1974); simulation of breeding programmes (e.g. CHOO and KANNENBERG 1979, WRIGHT 1980); minimizing the risk of loosing desirable genotypes (YONEZAWA and YAMAGATA 1978, WEBER 1979); exploring the limits to selection (e.g. BAILEY 1977, SCHWARZBACH 1979). All of these approaches should be studied further, and this also with regard to the mutual relations of their conclusions reached as to given cases. Nevertheless I would agree with the statement made by SPRAGUE and EBERHART (1977) that the "formula to predict gain from selection is probably the most valuable tool provided to the plant breeder by statistical geneticists". A statement like this is, of course, justified only because quantitative genetics also provides for the necessary fundamentals to gain estimates of the genetic parameters required for practical applications (see e.g. COCKERHAM 1980, WEIR et al. 1980). Moreover, the formula of the expected response to selection proves so valuable because it can be extended to processes in which selection is to be performed in two or more stages (COCHRAN

1951, Utz 1969). For, only such extension opens the ways of harmonizing the dimensions of successive selection steps and of comparing alternative breeding methods as to efficiency.

Quantitative genetic studies intended for maximizing the expected response to selection may be carried out either for a particular breeding program by using ad hoc estimates of the variability parameters involved or, with a broader scope of application, by putting each of these parameters to a number of different values within a realistic range. The latter kind of study is likely to be more elucidating, even with regard to a particular program, because the influence of the size of the variability parameters is also investigated. In either case, however, the results of such studies are of value only to those breeders who are familiar with the quantitative genetic theory on which the results are based, and with the genetical pecularities of the breeding process they try to optimize.

Although the interest of the plant breeder understandably centres on the particular crop he is working with, I think he cannot get a better insight into the quantitative genetic base and the methodological implication of his doing than by studying the genetical and operational analogies as well as differences among the various categories and methods of breeding.

Zusammenfassung

Eine synoptische Studie der Methoden und Kategorien der Pflanzenzüchtung

Die allgemeine Methodik der Pflanzenzüchtung wird untersucht hinsichtlich der Punkte: Kategorisierung, Vergleichen operativer Prozesse, nutzbare quantitative Variabilität, Erhöhen der Selektionseffizienz, mögliche Hilfe seitens der quantitativen Genetik.

Die Zuchtmethoden werden nach dem Vermehrungstyp der resultierenden Sorten in vier „Züchtungskategorien“ eingeteilt, nämlich in Linien-, Populations-, Hybrid- und Klonzüchtung. Innerhalb der Methoden werden drei „Züchtungsphasen“ unterschieden: Beschaffung der Ausgangsvariation, Bildung der Sorteneltern, Prüfung von Experimentalsorten. Die gesamte quantitative Variabilität, die in verschiedenen Phasen einer Zuchtmethode genutzt werden kann, wird untersucht an der jeweiligen „Sortenpopulation“, das ist die hypothetische Gesamtheit aller zu Beginn produzierbaren Sorten gegebenen Typs. Alle Züchtungskategorien bieten Möglichkeiten zur Ausnutzung des Vorteils einer Auslese zwischen Eltern anstelle einer Auslese in hierarchischen oder faktoriellen Systemen von Nachkommen solcher Eltern. Als hilfreichstes quantitativ-genetisches Instrument erscheint die Vorhersage des ein- oder mehrstufigen Selektionserfolges, mittels dessen sich qualitative und quantitative Alternativen innerhalb der Züchtungskategorien auf Effizienz vergleichen lassen.

Thanks are due to Drs. H. C. Becker, A. E. Melchinger, Gitta Oettler, R. K. Singh, and H. F. Utz for critical reading of earlier versions of this paper.

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