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BREEDING SYNTHETIC VARIETIES OF CROP PLANTS

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I. INTRODUCTION

Synthetic varieties are grown in a wide range of crop species including cereals, grasses, oilcrops, forage legumes and some tropical crops. Among these crops there are large differences as to natural mating system, to the amount of seeds produced by a single plant, and to the possibilities of asexuell reproduction. A review on breeding synthetic varieties cannot consider all of the many specific modifications of the basic breeding scheme which are feasible and might be necessary. The main purpose of the present review will be to outline the theory of breeding synthetic varieties; some generalizations and simplifications are inevitable.

The theoretical framework for breeding synthetics traces already back to Sewall Wright[1] in 1922, but a more advanced theory including polyploidy, epistasis, and self-fertilization is only recently available, elaborated mainly by Busbice[2,3], Gallais[4,5,6], and A.J. Wright[7,8].

To start with, the term "synthetic variety" will be defined, and the interrelations between synthetics, open-pollinated varieties and hybrids will be discussed. This is followed by a section which deals with the various steps of a very general breeding scheme for synthetic varieties. Finally, some of the specific problems are considered when this general scheme is applied to different crop species.

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II. GENERAL CHARACTERISTICS OF SYNTHETIC VARIETIES

Two examples for a breeding scheme of synthetic varieties are given in Fig. 1; the left one applies for a crop where clonal propagation is possible (e.g. alfalfa), and the right one for situations where inbred lines are available (e.g. maize). These two schemes obviously are based on the same principle ideas and the differences between them are chiefly of technical character. The first proposals for breeding synthetic varieties in this manner were made about 1940[9,10,11], but very similar approaches were already used by some maize and rye breeders in the beginning of our century[12,13].

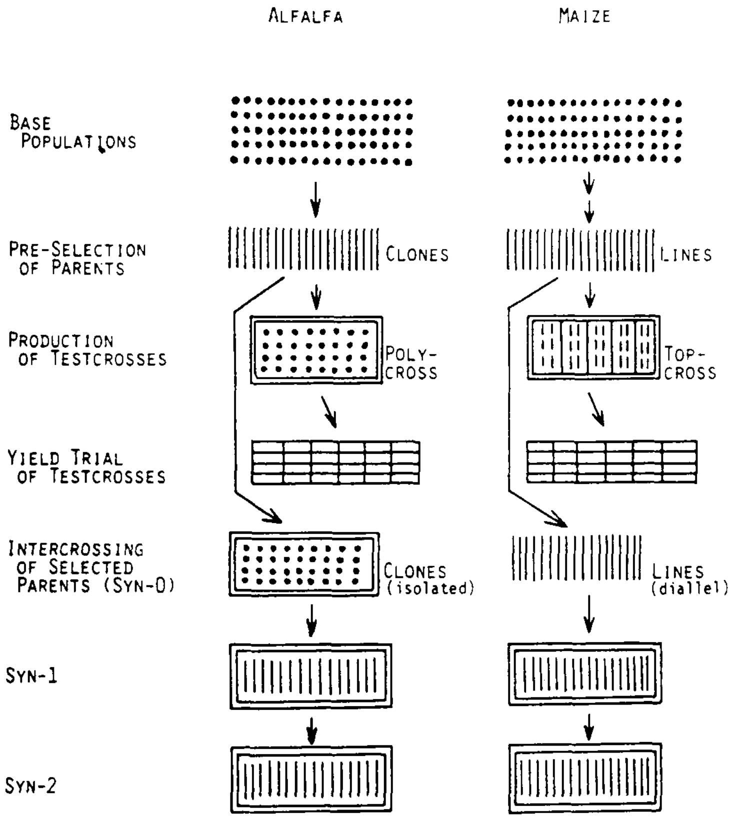

Fig. 1: Breeding synthetic varieties from clones (e.g. alfalfa) and lines (e.g. maize), respectively (adapted from re. 48)

Before going into more detail, some general remarks may be useful on the relations between synthetic varieties and other types of varieties. As suggested by Schnell[14,15] and Simmonds[16], all varieties can be classified into four categories according to the reproductive process used for propagation: clone varieties in vegetatively propagated crops, line varieties in self-pollinated crops, population varieties in cross-pollinated crops, and hybrid varieties, which are produced by artificially crossing of two parents.

To discuss the position of synthetic varieties within this systematization, Fig. 2 presents a general scheme of breeding naturally cross-pollinated species. The basis of any breeding program are one or several breeding populations[17,18]; that may be varieties, populations derived by crossing different varieties, or sometimes collected wild material.

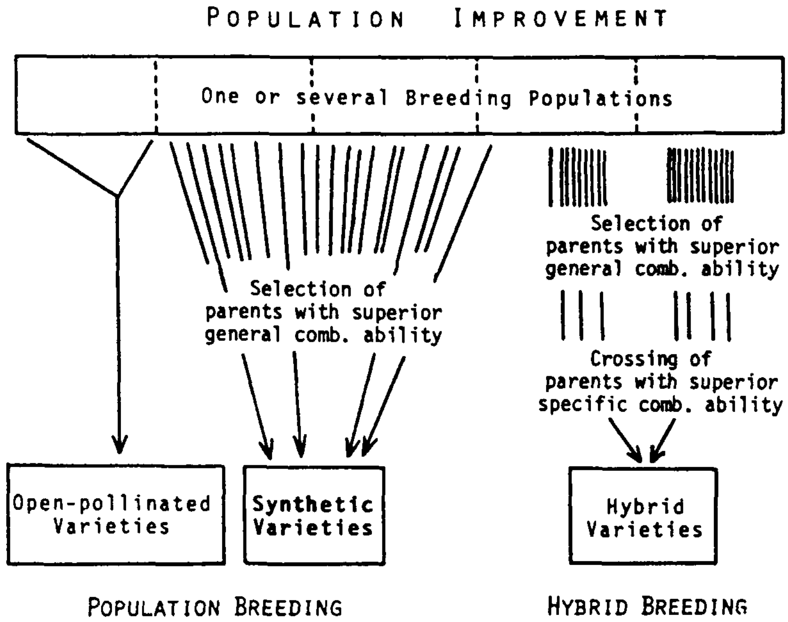

Fig. 2: General scheme for breeding cross-pollinated crops

From these base materials two principally different types of variety can be developed. The seed of population varieties is produced by uncontrolled cross-pollination under isolation, whereas the seed of hybrid varieties results from a controlled cross between two parents and cannot be multiplicated after that. Synthetic varieties are a special kind of population varieties, and a distinction between them and open-pollinated varieties sometimes is difficult.

In the typical case, a synthetic variety can be distinguished from other population varieties by three characteristics:

1. the parents of a synthetic variety are selected due to general combining ability (gca), and the base generation Syn-0 entirely consists of these selected parents, whereas in open-pollinated varieties the selected parents have been fertilized by pollen of unselected plants,
2. the number of parents in a synthetic variety is usually very restricted,
3. the parents are maintained and the variety can be regularly reconstituted from them.

At least as to the first two of these characteristics however, there exists no sharp line between open-pollinated varieties and synthetic varieties. In many cases, the parents for synthetics are selected not exclusively due to their gca, and on the other hand the breeding of open-pollinated varieties implies selection for gca too, though in a less efficient way. And as to the second criterion mentioned, of course it is arbitrary to suggest any fixed number of parents to separate synthetic from open-pollinated varieties.

Consequently, only the last of the three points provides an unequivocal definition of 'synthetic variety'[19], and thus in present textbooks[16,20], synthetics usually are defined as varieties which are regularly resynthezised from their components. This definition is very clear, but it does not point to the specific features in breeding methods of synthetic varieties, for most of the following theory can as well be applied to varieties which are maintained by continuous open pollination. The selection theory of synthetics is mainly characterized by the fact, that the variety results from a very restricted number of parents[21]. If this number becomes large, evaluation and selection of parents does not differ from the methods used in population improvement.

III. PRINCIPLES OF BREEDING SYNTHETIC VARIETIES

A very general scheme of breeding synthetic varieties is given in Table 1. To each step in this scheme there corresponds a critical question to which different answers are possible. In spite of the long history of breeding synthetic varieties, all these questions are still controversially discussed. In the following this five breedings steps will be dealt with as well from a theoretical point of view as from experimental evidence.

Table 1 General scheme for breeding synthetic varieties (modified from re. 19)

Breeding step	Critical question
1. Development of potential parents	Which genetic form of component should be used as parents?
2. Selection of superior parents	Which methods should be used to evaluate the parents?
3. Recombination of the best parents (Syn-0)	How many parents should be combined?
4. Further multi-plication of Syn-1 by open pollination	How many generations of multi-plication should follow before use as commercial seed?
5. Maintenance of the synthetic variety	Should the variety be maintained by open pollination or regularly be reconstituted from the parents?

1. Development of potential parents

Various genetical forms can be used as potential parents to construct synthetic varieties. Generally, three types of parents can be distinguished: clones, inbred lines, and various forms of narrow populations.

The use of clones is most common in herbage grasses and many forage legumes. The vegetative propagation is an easy and save way to maintain a specific genotype without genetic changes. Thus the final variety can be build up exactly from the same genotypes which were examined during the testing phase. Of course, the use of clones is restricted to crops which can be assexuelly propagated. May be, that in future new methods of cell culture technique will open new possibilities for species, in which clonal propagation today is impossible or difficult.

If the production of clones is difficult, inbred lines can be used instead. The gametes formed by a single genotype are equivalent to the gametes produced by his progeny after one generation of selfing (S_1-line), and thus o

a synthetic from S_1-lines is expected to be very similar to a synthetic build up from the cloned genotypes of the S_0-generation. The use of higher generation inbred lines can be advantageous due to the increase of genotypic variance during inbreeding. Therefore sometimes it was proposed to use inbred parents even in crops which can be easily cloned like alfalfa[22,23] or cocksfoot[24].

In many crops the production of inbred lines is difficult due to self-incompatibility. Sometimes the self-incompatibility system can be overcome temporarily, e.g. in rye by a heat treatment before flowering[25]. Alternatively, inbred lines of self- incompatible plants can be developed by sib-mating[26].

Usually, self-incompatibility is not complete, and genes for self-fertility exist in many populations. By selecting for seed set under isolation, e.g. self-fertile rye material can be easily developed[18]. But the use of self-fertile material in a naturally self-incompatible species may be risky; self-fertile plants may show a certain amount of self-pollination instead of complete random mating, if multiplicated by open pollination.

In rye it was observed, that synthetics from self- fertile material yielded about 10 to 15 % less than comparable populations of self-incompatible material[27]. The average amount of self-pollination in self-fertile rye populations was estimated to be between 35 and 40 %[27,28]. In alfalfa, similar investigations in the role of self-fertility gave unequivocal results. It was observed, that synthetics from highly self-fertile clones were inferior to self-incompatible material[29], but in other experiments, no such relationship occurred[30].

In conclusion, the use of self-fertile material should be strictly avoided in breeding synthetic varieties except complete outcrossing can be guarantied. Generally, incompatibility systems aroused during evolution as a protection from inbreeding depression due to self-pollination, and it will always be a risk to abandon this natural protection mechanism.

Consequently, if a self-incompatible species is not easy clonable, the only way to construct synthetics will be the use of narrowed populations. The "narrowest" population is a full-sib progeny derived by crossing two genotypes. More often used is the seed of one open pollinated plant or clone , i.e. half sib progenies. Of course, any broader type of populations can be used to form the variety too.

When comparing the various possible forms, the genetic variance is expected to increase from populations via half-sib progenies, full-sib progenies, S_1-lines or clones to homozygous inbred lines. But the effort necessary to obtain and test a large number of parents increases in about the same order. Thus the decision, what type of parent should be used largely depends on the biology of the crop, on a number of technical considerations, and on the question, wether the breeding of synthetic varieties shall be integrated into a breeding program for open-pollinated or hybrid varieties.

2. Selection of parents

Before synthetic varieties can be constructed, a very rigourous selection of parents is necessary, for e.g. only 10 parents can already be combined in more than 1000 different ways. The selection of parents can be based on different informations: the *per se* performance, the general combining ability (gca), and the specific combining ability (sca).

The first synthetic varieties were developed by selecting parents with outstanding *per se* performance in protein content, winter-hardiness, disease resistance etc. A recent idea in this connection is to select several components with different resistance genes and to combine them in one synthetic variety[31,32]. This is in straight analogy to the multiline concept in breeding self-pollinated crops.

In most breeding schemes for synthetic varieties, the evaluation of the *per se* performance is only the first stage of selecting parents, and is followed by a gca-test (cf. Fig. 1). The gca-effects can be estimated either by polycross- or by topcross-tests.

The polycross-test appears to have been developed independently by Frandsen[10,33] with timothy, by Tysdal and coworkers[11] with alfalfa, and by Wellensiek[34,35] with rye. To assure random pollination, originally it was proposed to plant each clone at 20 different places in an isolated polycross-block, but the number of replications per clone probably can be reduced to about 10[36-38]. If the number of replicates per clone is chosen to be identical with the number of different clones included in the polycross, systematic designs can be used. Systematic field plans immediately available for use have been published[39] for 12 different numbers of clones between 6 and 46.

The number of replications per clone could in principal be reduced to only one plant. Some authors[40,41] regard the progeny of just one open pollinated plant to be sufficient for a reasonable good gca estimate. From their point of view, the main purpose of the polycross is to produce seed, and often ten or more plants of each clone will be necessary to get enough seed for a yield trial sown under realistic planting densities and over a number of locations.

For estimating the gca-effects, a top-cross test is often used instead of the polycross-test. The opcross-test was developed by maize breeders, for it is much easier to emasculate maize plants and let them be pollinated by a tester, than to lay out a polycross-block. If artificial emasculation is more difficult than in maize, several other possibilities exist to produce test seed; e.g. in rye this was done by excess of tester pollen, or by use of testers which contain a marker gene or are either self-incompatible or cytoplasmic male sterile[42].

The differences between polycross and topcross are more technical than genetical ones. If a mixture of all parents is used as topcross tester, the two tests are completely equivalent. Consequently, the results of topcross and polycross test have been found to be highly correlated[29,43,44].

The most complete evaluation of parents is to intercross them in a diallel fashion. From a diallel test, as well gca as sca effects can be estimated. Diallel crosses are frequently included in research projects, but this laborious design has probably never been used for practical breeding.

To discuss the various possibilities of selection, the expected yield of a synthetic variety has to be regarded. The expected yield Y of a synthetic in equilibrium was already given by S. Wright[1] :

$$Y = C - \frac{C - S}{n} \qquad (1)$$

where C is the mean of all possible crosses between parents, S the mean of all intra-parent progenies, and n the number of parents. The intra-parent progeny is the progeny of one parent when propagated *intra se* under complete isolation. If the parent is a homozygous line, a S_1-line or a population, S means the performance of the parent itself, if the parent is a heterozygous clone, S is the performance of the progeny of this clone after one generation of selfing.

Formula (1) assumes absence of selection, absence of epistasis, and diploidy. Epistatic effects can be included in the prediction[6,8,21], but this requires additional informations on e.g. F_2 or Syn-2 generations, which usually are not available.

For non-inbred polyploid parents, formula (1) can be extended[6] :

$$Y = C - \frac{2k - 1}{k} \, \frac{C - S}{n} \qquad (2)$$

where k is the level of polyploidy (1 = diploid, 2 = tetraploid, 3 = hexaploid etc.)

The reliability of formulas (1) and (2) have been confirmed experimentally as well for diploids[45-47] as for polyploids[6,30]. The use of these formulas requires the performance of all possible crosses between the parents, that means the results from a complete diallel; but even if these data are not available, these two formulas are very useful to discuss the efficiency of a selection based only on gca values.

As can be seen from formula (1), the performance of a synthetic variety depends not only on the gca, but also on the term (C-S)/n which specifies the amount of inbreeding resulting from the limited number of n parents. To take into account this inbreeding, the concept of general varietal ability (gva) was introduced by Wright[7] and Gallais[5].

The gva is a combination of the gca and the performance after inbreeding, and the inbreeding depression is included the more the smaller the synthetic is. The magnitude of gva-effects thus depends on the size n of the synthetic, and for a parent i and a synthetic from n parents it is given for diploids by[7]:

$$gva(n)_i = \frac{1}{n} \left(2gca_i - \frac{2gca_i - l_i}{n} \right) \qquad (3)$$

and for noninbred polyploid parents by[5] :

$$gva(n)_i = \frac{1}{n} \left(2gca_i - \frac{2k-1}{k} \frac{2gca_i - l_i}{n} \right)$$

where l_i is the effect of the intra-parent progeny, that means $(S_i - S)$.

In analogy to the concept of gca and sca the general varietal ability gva can be supplemented by an effect of the specific varietal ability (sva). The sva of the combinations of parents i and j for a synthetic of the size n is

$$sva\ (n)_{ij} = \frac{1}{n^2}\, 2sca_{ij} \qquad (4)$$

If there is a given number of available components, and among these components n are selected for a synthetic variety, the expected yield of this variety is:

$$Y = \mu(n) + \Sigma gva(n)_i + \Sigma sva(n)_{ij}$$

By inserting formulas (1), (3) and (4) we get

$$Y = C - \frac{C-S}{n} + \frac{2(n-1)}{n^2} \Sigma gca_i + \frac{1}{n^2} \Sigma l_i + \frac{2}{n^2} \Sigma sca_{ij} \qquad (5)$$

It was shown experimentally, that the yield prediction of synthetic varieties can be considerably improved, if the performance of the parents after selfing (l_i) is included according to formula (3)[6,30,48]. There is a large genetic variability in the amount of inbreeding depression[24,49,50], and parents with small inbreeding effects are preferable. As can be seen from formula (5) however, the coefficient of the l_i-effects is $1/n^2$; that means, if n increases, the influence of the parental performance decreases, and the gva is nearly completely determined by the gca.

Beside this, the importance to consider both gca_i and l_i is somewhat diminished by the fact, that these two effects are positively correlated. Theoretically, this correlation between gca_i and l_i should be at least medium[51] or even very high[21]. Experimentally however, for yield the respective correlations were found to be usually rather low[17,52-56].

As can be seen from formula (5), the influence of the sca-effects rapidly decreases if n increases. Moreover, with n parents there are $n(n-1)/2$ different sca-effects, and it is very unlikely to find a larger number of parents with positive sca-effects for all possible combinations among them.

In conclusion, the parents for a synthetic variety can be reliable selected by testing their gca, if n is large enough. Only if a genetically very narrow synthetic with no more than three or four parents in intended, a test of intra-parent progenies and perhaps of sca-effects too will give valuable additional information.

3. Recombination of the best parents

To determine the number of parents to be combined, two points have to be regarded. The first is the inbreeding in the synthetic variety; this effect can be reduced by increasing the number of parents. But a second point to be considered favours small numbers of parents; for with a smaller number of parents a more intensive selection can be applied and only the best parents are included in the synthetic variety. In other words, with increasing number of parents, the mean of all synthetic varieties will increase, but the variance between them will decrease[4,57]. These considerations lead to the general conclusion, that there must be an optimum number of parents.

Generally, this optimum number should depend on the material used. This number will be larger if many parents with high gca are available than in a small material with only few good parents. Beside this, the genetic form of the parents has to be regarded. In diploids, the amount of inbreeding in a synthetic formed from homozygous lines is equivalent to the inbreeding in a synthetic from only half the number of parents, if these are heterozygous (cones or single crosses). This can be easily seen, for from e.g. 8 inbred lines 4 nonrelated single crosses can be produced, and a synthetic variety from the 8 inbred lines is equivalent to a synthetic from the 4 single crosses[58]. Generally, to get the same effective population size and thus a comparable level of inbreeding, the number of parents must show a ratio of 1 : 2 : 4 : 8 when using half-sib progenies, full-sib progenies, clones (or single crosses of inbred lines or S_1-lines), and homozygous inbred lines, respectively.

As to polyploid crops, a synthetic made from heterozygous tetraploid clones should show only one quarter of the inbreeding in a synthetic from diploid homozygous lines[2,54]. With different assumptions on the interactions between more than two allels however, the inbreeding in polyploid synthetics can be equal or even higher than in diploids[22].

A large number of experimental investigations on the optimum number of components can be found in literature. The results are summarized in Table 2. In most experiments the optimum number of components was about 5, and never the use of more than 10 clones was recommended. The level of polyploidy had no influence on these recommendations. Many authors reported the differences between synthetic varieties to be rather small, if the number of components was varied within certain limits.

The practice of the breeders is not in complete agreement with these recommendations. Fig. 3 shows the distribution of the number of parents in synthetic alfalfa varieties registered in U.S.A. Table 3 gives the number of clones in released varieties registered in USA[59] and in France[60] respectively. It is obvious, that breeders use a wider range of numbers than recommended from the research experiments. About 40 % of all varieties covered were constructed from more than 10 components.

This again reflects, that the optimum number mainly depends on the material used. If a large number of clones with similar high gca is available, the optimum number can well be more than ten. This may explain the trend in the USA to increasing numbers of parents[20]. In several of the scientific experiments listed in Table 2, only synthetics with 2 to 6 clones were included, and the 'optimum' number recommended was the largest number investigated experimentally.

Table 2 Experimental studies on the optimum number of parents in synthetic varieties (adapted from refs 59 and 60)

Level of Ploidy	Species	Recommended no. of parents	Refs
diploid	Zea mays	4-6	47
	Zea mays	6-9	59
	Secale cereale	3-8	115
	Lolium perenne	4	116
	Lolium perenne	6	117
	Lolium multiflorum	8	118
	Festuca pratensis	5-10	72
	Trifolium pratense	8	119
tetra-ploid	Medicago sativa	2-4	120
	Medicago sativa	2-6	53
	Medicago sativa	4-5	121
	Medicago sativa	2-4	122
	Medicago sativa	4-9	123
	Medicago sativa	4	30
	Medicago sativa	8	124
	Dactylis glomerata	4-10	125
	Dactylis glomerata	4-8	126
	Dactylis glomerata	5-10	72
hexa-ploid	Phleum pratense	4-10	127
	Phleum pratense	5-10	72
octo-ploid	Bromus inermis	4	128

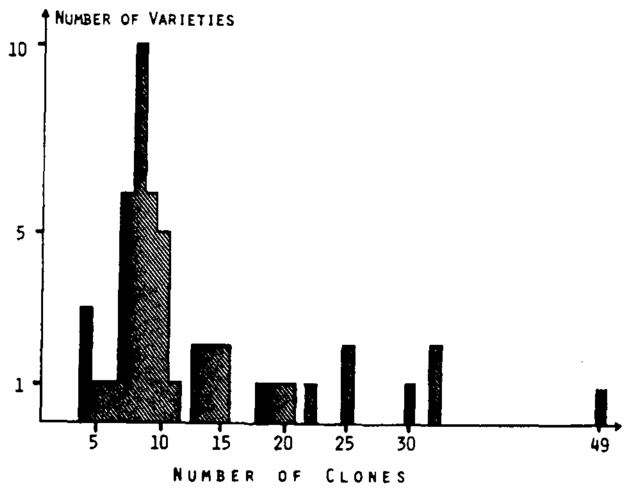

Fig. 3: Number of clones in synthetic varieties of alfalfa registered in USA (from re. 59)

Table 3 Number of clones in registered synthetic varieties of forage crops (adapted from refs 59 and 60)

No. of clones	Number of varieties USA	France	Total No.	%
-5	11	25	36	23.7
6-10	38	17	55	36.2
11-20	17	11	28	18.4
21-40	12	11	23	15.1
41-100	2	8	10	6.7

For any given material, the optimum number of synthetics can be estimated, when the performances of all possible synthetics are predicted by formula (5) and the combination with the highest yield is determined[47,59,61].

For many practical purposes, formula (5) can be substituted by a simplified formula, where differences in l_i and sca_{ij} are neglected[42,59] :

$$Y = C - \frac{C - S}{n} + \frac{2(n-1)}{n^2} \Sigma gca_i \qquad (6)$$

To use this formula, it is only necessary to know the gca effects of the parents and to have a general estimate of the average yield of the crosses (C) between parents and the average performance of the intraparent progenies (S). Usually at least rough estimates for these values are available. A prediction based on formula (6) is in very close agreement to predictions based on formula (5), if the number of parents exceeds three or four[59,61]. Thus in most cases the optimum number of components can be determined for any given breeding material by formula (6), and only gca-estimates are required for this procedure.

So far, the optimum number of components was discussed regarding only yield performance. But beside this, some other aspects have to be considered. Usually, a phenotypic similarity of the clones is necessary to satisfy legislative requirements for uniformity and distinctness, and this often will severely restrict the number of clones available. In synthetic varieties constructed from very few parents, yield stability on the other hand may be inferior to broader based synthetics[62,63]. Beside this, in very small synthetics sometimes unpredictable changes from generation to generation were observed, as well in yield[64] as in morphological appearance[65]. Finally, if clones are maintained vegetatively to reconstruct the variety regularly, there is always the risk to loose one of them by disease attacks, and the breeder can overcome such a loss only if the number of clones is not too low.

4. Further multiplication

The expected yield of a synthetic in advanced generations was described most generally by Busbice[3]. In a generation t the expected performance Yt is

$$Y_t = A + (1-F_t)B \qquad (7)$$

where Ft is the coefficient of inbreeding in generation t, A is the performance of complete homozygous parents (F=1), and B is the amount of heterosis, that means (C-A).

This formula assumes a linear relationship between performance and coefficient of inbreeding F_t. Such a linear relationship is expected if no epistasis exists, competition effects are of no importance, and if no interactions between more than two alleles have to be considered in polyploids. If these assumptions hold valid, formula (7) is useful for any situation where F_t can be given; thus polyploidy, partial self-pollination and inbreeding of the parents can be taken into account[2]. In fact, formula (7) is a generalization of the Sewall-Wright formula (1), as can be seen if it is expressed as

$$Y = C - F_t(C-A)$$

with C as the performance with complete heterozygosity.

To derive the values of F_t, two different possibilities to establish the syn-1 have to be distinguished:

a) Random mating; that means that if the syn-0 consists of n parents, each plant will be pollinated by a different plant of the same parent with the probability of 1/n.
b) Controlled crossing; that means that the above mentioned fertilizations between plants of the same parental components are excluded from forming the syn-1. This is the case if self-incompatible clones are used, or if the parents are intermated artificially.

If possible, a controlled crossing in Syn-0 is preferable; if the parents are sown in mixture and seed is produced by open-pollination, different components may contribute very different amounts of pollen and different numbers of seeds.

In some exceptional cases the syn-1 of two self-incompatible clones is directly used as commercial seed[16]. In this case, the seed only consists of hybrids between the two genotypes and consequently should be considered as hybrid variety instead of a synthetic variety.

According to Busbice[2] and slightly modified[66], the amount of inbreeding in the syn-1 from n unrelated parents can be given as follows:
a) with random mating

$$F_1 = \frac{1}{4k-2}\,[s + (1-s)/n]\,[1 + (2k-1)F_0] + \frac{k-1}{2k-1}F_0$$

b) with controlled crosses

$$F_1 = \frac{k-1}{2k-1} F_0 \tag{8}$$

with
k = level of polyploidy (1=diploid, 2=tetraploid, etc)
F_0 = coefficient of inbreeding of the parents
s = amount of self-fertilization

In the following generations, the coefficient of inbreeding is be given by

$$F_t = \frac{1 - z^{t-1}}{(2k-1)(1-z)} \left[\frac{s}{2} + k(1-s)r_1\right] + z^{t-1}F_1 \tag{9}$$

with

$$z = \frac{s}{2} + \frac{k-1}{2k-1}$$

r_1 = coefficient of relationship in syn-1

$$= \frac{1 + (2k-1)F_0}{2kn}$$

These formulas are rather complex, for they are very general. If we only consider completely out-crossing species (s=0), rather simple expressions can be derived.

In diploids (k=1) and with random mating, F_t is constant for all generations:

$$F_t = \frac{1 + F_0}{2n} \tag{10}$$

If the syn-1 is produced by controlled crossing, from (9) follows $F_1 = 0$; that means the syn-1 is non inbred as to be expected. In this situation formula (10) is valid for syn-2 and all following generations. If homozygous lines are used as parents ($F_0 = 1$), $F_t = 1/n$, and inserting this in formula (7) leads to the Sewall-Wright formula (1).

Whereas in diploids a Hardy-Weinberg equilibrium is reached after the first generation of random mating, this is not the case in polyploids. Consequently the performance of synthetic varieties of polyploids is expected to change from generation to generation. In the most common case of noninbred parents which are self-incompatible, the coefficient of inbreeding in the syn-1 is 0 and in the following generations it can be given by

$$F_t = \frac{1 - (1/3)^{t-1}}{4n}$$

for autotetraploids and by

$$r_t = \frac{1 - (2/5)^{t-1}}{6n}$$

for autohexaploids.

In the following, we will compare the above derived expectations with experimental results. Table 4 summarizes experiments with synthetic varieties in diploid crops. Relative yields are given from syn-1 (=100) to syn-3 or syn-4. In the last three experiments listed in the table, homozygous lines were used as components, and the first generation of yield test was the syn-2. All other synthetics were constructed from clones.

Table 4 Relative performance of advanced synthetic generations in diploid crops

Formation of Syn-1	Crop	Syn-1	Syn-2	Syn-3	Syn-4	Refs
Random mating	Secale cereale	100	99	99		56
Crossing	Secale cereale	100	94	94		66
	Trifolium prat.	100	100	99	100	129
	Lolium perenne	100	-	89	77	130
	L. multiflorum	100	94	95		64
	Festuca pratensis	100	103	105		64
	Festuca pratensis	100	98	96		72
	Zea mays	100	93	84	81	68
	Zea mays		100	101	101	45
	Zea mays		100	103	100	69
	Zea mays		100	92	86	69

If the syn-1 is constructed by crossing, the yield decreases in all experiments from syn-1 to syn-2 as expected. After the first generation of random mating, the performance should be constant. As can be seen from Table 4, this seems to be true in most of the experiments; but in some exceptions there was a remarkable yield decrease following syn-2 or even syn-3. In these cases the assumptions of the theoretical considerations are obviously not fulfilled.

The most critical assumptions are absence of selection and absence of epistasis. To assume no natural selection is obviously unrealistic under many circumstances, and mass selection was shown to be effective to increase yield in advanced generations of maize synthetics[67,68,69]. By analysing isozyme polymorphism in Lolium perenne[70] changes in gene frequencies were detected within few generations of uncontrolled multiplication.

The effect of epistasis in advanced generations can be positive or negative depending on the assumptions[8,66]. A yield decrease due to epistasis is expected if parents from different populations are combined, and if the performance of these source populations is partly due to favourable epistatic effects.

The possible role of epistasis was especially evaluated in an experiment with maize[69]. From two very distinct base populations inbred lines were developed without severe selection. If lines originating from the same base populations were combined, the yield of the synthetics was stable up to syn-5. But if lines from the two different source populations were included in the same synthetic, a remarkable yield decrease from syn-2 to syn-4 of about 14 % was observed.

We will now turn to expectations for autopolyploid crops. As already pointed out, in polyploids even without selection and epistasis there are changes in performance to be expected following syn-2. If constructed from non-inbred parents, the performance could slightly decrease in advanced generations due to an increase in the inbreeding coefficient F_t. If the parents themselves are inbred, on the contrary, maximal heterozygosity is not yet obtained after one generation of random mating, and in advanced generations a further increase in yield can be expected.

To illustrate these situation, Fig. 4 shows the expected yields for different numbers of parents, based on formulas (7) and (9) and assuming that A is 50% of C. It is quite obvious, that the expected changes in most cases are rather small, especially if the number of components is not very low. These expectations assume absence of epistasis and natural selection. With epistasis, from syn-1 to the following generations performance can decrease or increase depending on the type of epistatic effects involved[71].

Experimental investigations of advanced generations of polyploid crops are summarized in Table 5. If the syn-1 arises from non-inbred clones, which are usually self-incompatible, a slight decline can be observed from syn-1 to syn-2. This decline usually was not found, if the number of clones exceeds about five[72,73]. All further changes following syn-2 are very small and non-significant.

The construction of a synthetic by random mating of partly inbred strains or lines is not very common. In the two experiments included in Table 5, the yield increased from syn-1 to syn-2 as expected from theory.

In conclusion, most of the published data support the validity of the theory outlined. Nevertheless, there are examples of unpredictable changes in performance in advanced generations of synthetic varieties. From experimental evidence the danger of an unexpected yield decrease during multiplication seems to be larger in diploid than in polyploid species.

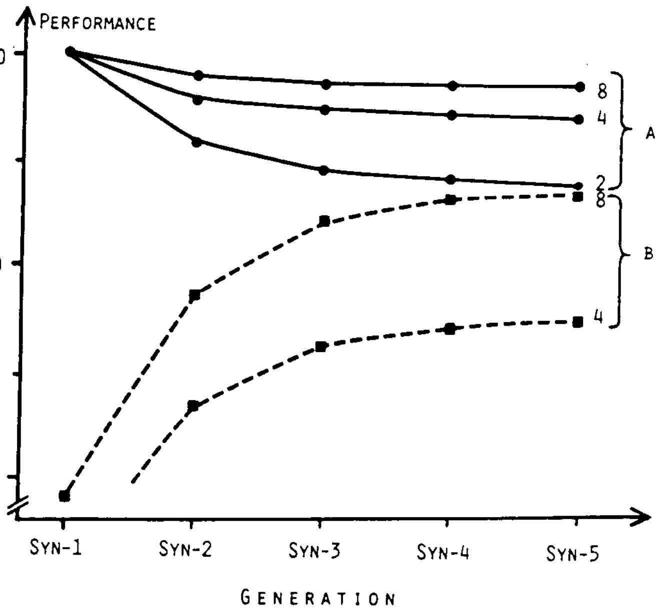

Fig. 4: Expected relative performance (C=100) of tetraploid synthetic varieties constructed from different numbers of parents (2,4,8).
A = Syn-1 produced by crossing heterozygous parents
B = Syn-1 produced by random mating of homozygous parents

Table 5 Relative performance of advanced synthetic generations in polyploid crops

Type of Parents	Crop	Syn-1	Syn-2	Syn-3	Syn-4	Refs
Clones (non inbred)	Dactylis glomerata	100	91	87		50
	Dactylis glomerata	100	97	95	95	72
	Medicago sativa	100	94	93	92	53
	Medicago sativa	100	95	94	94	131
	Medicago sativa	100	97	99		64
	Medicago sativa	100	99	98		72
	Fest. arundinacea	100	97	99		64
	Phleum pratense	100	95	94		72
Lines (inbred)	Secale cereale	100	108			132
	Medicago sativa	100	105	104		133

Finally we will shortly consider crops which are partly self-fertilized like some species of *Brassica* and *Vicia*. Using formula (9), some general expectations can be derived[2,66]; we only consider parents which are inbred, for this will generally be the case in breeding partly autogamous crops. If the syn-1 is produced by artificial crossing, the yield will decrease in the following generations; if the syn-1 is produced by random mating of inbred lines on the contrary, maximal heterozygosity is not yet obtained in syn-1, and the yield is expected to further increase in advanced generations. The last of these two expectations was confirmed experimentally. From syn-1 to syn-2 an average yield increase of 6 % in *Brassica napus*[74] and of 6 to 7 % in *Sinapis alba*[74,75] was observed.

5. Maintenance of the variety

Generally there are two possibilities to maintain a synthetic variety. The first is to maintain the components and reconstitute the variety regularly from them. As already mentioned, many authors restrict the use of the term "synthetic variety" to varieties which are periodically reconstituted in this way. The alternative approach is to treat the synthetic like an open-pollinated variety and maintain it continuously as random mating population.

If the synthetic is constructed from a small number of parents it may be regarded more convenient to maintain the parents themselves than the complex population, for it is easier to detect off-types in multiplications of clones or inbred lines than in an open-pollinated population. Sometimes breeders prefer to produce the syn-1 on a large scale and store the seed. In the following years the advanced generations are produced by going back to the stored syn-1.

If tolerated by legislative regulations, it is possible to improve the variety instead of just maintaining it. For this purpose, some of the parents can be replaced by better parents when reconstructing the variety in later cycles[32].

In maize, already Jenkins[9] proposed to combine the breeding of synthetics with a program of recurrent selection by using the syn-1 or syn-2 as source for the next cycle of selection. Similar procedures were proposed e.g. in herbage grasses[33], alfalfa[54,76] and rye[56,77]. This combination of synthetic varieties with recurrent selection again demonstrates the close similarity in breeding synthetic and open-pollinated varieties.

IV. SYNTHETIC VARIETIES IN VARIOUS CROPS

The many crop-specific problems when breeding synthetic varieties cannot be thoroughly discussed but just mentioned, and some references to the literature will be given. Extensive reviews articles exist e.g. for grasses[41,78,79], alfalfa[80], maize[17], and rye[42].

1. Herbage grasses

Most grasses can be easily cloned, and the clones can be kept for several years. Thus in many countries synthetic varieties are the most common type of variety; e.g. in the Fed. Rep. of Germany in 1981, 137 synthetic varieties were registered, compared to only 101 open pollinated, 24 apomictic and 1 hybrid varieties[81].

The originally proposed method to test for gca was the polycross[10,82], but at present often topcrosses are preferred. The topcross test is less labour intensive, and a visual observation of the clone performance is possible[44].

A special difficulty in predicting yield of synthetic varieties is caused by competition between genotypes, which in herbage grasses is by far more pronounced than in cereals. Attempts have been made to take into account competitive effects[83]. Beside this, the estimates of gca-effects may be biased due to maternal effects[84].

2. Forage legumes

To illustrate the breeding of synthetic varieties, textbook authors often chose alfalfa as example. Starting from Tysdal and coworkers[11], alfalfa has become one of the main objectives for basic research on breeding methods for synthetic varieties[22,23,30].

Alfalfa is easily clonable, and as a consequence usually clones are used as parents and the selection is based on the performance of the polycross test. In other forage legumes however, the maintenance of clones for a number of years is more difficult, and synthetic varieties have to be constructed from S_1-lines or from remnant polycross seed.

3. Maize

Maize is one of the crops, where synthetic varieties have a very long tradition. Hayes and Garber[12] proposed already in 1919 to construct varieties by combining high protein inbred lines, and in 1940 Jenkins[9] used S_1-lines which were selected due to the performance of their polycross progenies. The use of synthetic varieties was proposed at that time mainly for low-income areas of the world to eliminate the need for farmers to purchase new F_1-hybrid seed each year[67].

At present, it is more common to combine heterogenous strains instead of inbred lines. Though in this case many authors prefer the term "composite variety" instead of synthetic, the principal breeding methods do not differ and formulas given in section II can be applied in this situation too[17]. Composites are one of the types of variety favoured by CIMMYT[85] and especially common in several African countries[68,86-88].

Establishing the parents by one or more generations of artificial self-pollination may include the risk of unconscious selection for genotypes which tend to increased self-fertilization. Protandry, which is the natural protections against self-fertilization in maize, does no longer exist in material developed by continuous artificial selfing; and no information seems to be available on the consequences of this on the amount of self-pollination in maize populations.

Synthetics in maize are not only used as commercial varieties but also as important gene sources in hybrid breeding programs. An example for this possibility of use is the famous 'Iowa Stiff Stalk Synthetic' (BSSS) which was synthesized in 1933 by G.F. Sprague from 16 lines with resistance to stalk breakage. The BSSS was continuously improved since that time and today lines originating from this breeding population are extensively used in hybrids in the U.S. Corn Belt[17].

4. Rye

The breeding of synthetic varieties in rye is as long used as in maize and the first synthetic varieties from inbred lines were constructed in the beginning of our century[13,42]. But synthetics from inbred lines have never been very successful in this crop. This is most probably due to the fact, that the loss of the natural selfincompatibility system leads to an appreciable amount of self-pollination and thus inbreeding depression in the population.

More successful was the use of narrow populations of selfincompatible material. Varieties based on combining such narrow populations from different sources today are grown in several European countries.

5. Sugar beets

Synthetics were a common type of varieties in beets before hybrid breeding was possible. They were used in sugar beet breeding in Europe[89], USA[90,91], and Japan[92] and also in fodder beets[93].

Today, in sugar beets usually hybrid varieties are grown. In most hybrid breeding programmes, the pollinator parent is synthesized from a number of selected parents and propagated for several generations; no changes were observed from syn-1 to syn-5[94]. When using synthetic varieties as pollinator parent of a hybrid variety, the amount of inbreeding depression within this synthetic is irrelevant, for it is not grown by itself. In this situation, the value of the synthetic is completely determined by its combining ability to the sterile seed parents.

6. Field beans

Breeding of synthetic varieties in field beans was repeatedly proposed[95,96]. In this crop, the breeder has to work at the peculiar situation of a predominantly autogamous species. For this reason, the per-se performance of the components contribute more to the performance than the gca, and a combination of the informations on both li and gcai according to formula (3) seems especially promising. To maximal utilization of heterosis, a selection of lines with an high degree of outcrossing is desirable. This can be done by the use of a tester with a marker gene[96].

When compared to line varieties, the advantage of synthetics is not only their partial use of heterosis, but also the possible increase in yield stability[97].

7. Rape seed

Rape seed is a predominantly self-pollinating crop too, thus the remarks on field beans hold true here again. Synthetic varieties have been demonstrated to exceed there parental lines as well in yield[74,98] as in yield stability[99].

Rape seed is a crop, where competitive effects between different genotypes are of great importance[100] and consequence may be taken into account for selecting parents for synthetic varieties[99].

8. Others

Breeding of synthetic varieties is principally possible in all crops which are completely or partly outbreeding. Sometimes the term "composite variety" is also used in self-pollinating species where different genotypes are combined; but in this case the variety is a mixture of homozygous genotypes, and heterosis does not contribute to the performance as is the case in synthetic varieties.

Reports on breeding synthetic varieties can be found in literature for many crops, among them millet[101-103], sorghum[104,105], buckwheat[106], cotton[107,108], sunflower[109-111], mustard[74,75], poppy[112], rubber[113], and pigeon pea[114].

This list of crops cannot be discussed in details; but it finally underlines the wide applicability of the concept of breeding synthetic varieties.

V. SUMMARY

A synthetic variety is a type of population variety which is synthesized from a restricted number of parents. These parents are separately maintained and the variety can be identically reconstituted from them. The literature on breeding synthetic varieties is reviewed following a very general scheme of breeding methods.

The initial step in breeding synthetic varieties is the decision, which genetic form of parents should be used. It is possible to use clones, lines of different level of inbreeding, and more or less narrow populations, and it depends on a number of technical considerations which form is preferable. If possible, the material used has to be self-incompatible to prevent inbreeding.

If the genetic form of the parents is once determined, the following steps can be optimized. The yield of a synthetic variety can be reliable predicted from the general combining ability of the parents, unless the number of parents is very small (not more than 3 or 4). The optimum number of parents to be included can be calculated for any given material.

After the first panmictic reproduction, the yield of synthetic varieties should theoretically hardly change within the first generations of multiplication. There is experimental evidence however, that under certain circumstances an unexpected yield decrease may occur.

Finally, for some important crops, the specific problems and possibilities of synthetic varieties are shortly mentioned.

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