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Reproduction Mode and Crop Improvement*

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Summary. The author has tried to accumulate data on the reproduction modes of crop plants: autogamy and allogamy in the case of sexuality, involving self-fertility and self-sterility, and different means of vegetative propagation and apomixis. In combination with the state of ploidy and the basic chromosome number the different modes of reproduction exert a considerable influence on population structure and the success or failure of different methods applied in plant breeding. This relates to the use of selection, hybrid vigour (F_1 heterosis), gene recombination, as well as polyploidy and induced or spontaneous mutation. It is pointed out that extranuclear (cytoplasmic) inheritance should not be neglected as a device also in the case of polyploidy and mutation.

Transitional stages exist between autogamy and allogamy. Autogamy is obligate in no or at least very few cases. In allogamous species inbreeding and subsequent outcrossing are important features in their improvement by breeding. In dioecious, monoecious and hermaphroditic species the modes of reproduction can be switched into one another by appropriate methods of gene recombination, mutation and selection. Apomictic species, for instance several grasses, display a series of transitions between more or less obligatory apomixis (parthenogenesis and vivipary) and partial or complete sexuality.

At the end of the article data are presented to indicate how various modes of reproduction influence the methods applied in the exploration and conservation of plant gene pools.

Finally, the pioneer work on plant exploration carried out by VAVILOV, ZHUKOVSKY and their co-workers is emphasized. Favourable genes, chromosomes and cytoplasms present in natural populations have to be preserved. New favourable genes etc. should be continually produced by mutation. Preservation of old genes and induction of new genes are means of augmenting the breeders' resources in their efforts of continuous crop plant improvement.

1. Introduction

The methods of reproduction and propagation of cultivated plant species greatly influence the principles applied in their improvement by plant breeding. Moreover, in all kinds of phanerogams, wild, semi-domesticated or domesticated, the reproductive behaviour also affects population structure. Modes of reproduction are continually acted upon, changing or stabilizing, during evolution.

As far as we now know, new genotypes are produced in higher plants only by two means: (1) *mutation* (sensu lato) in (i) the number and (ii) the structure of already existing „molecules“ and units of heredity (chromosomes, genes inside as well as outside the cell nucleus), (2) *hybridization and subsequent recombination* of chromosomes and genes, old and new, by sexual (and/or asexual) means. Genotypes, incapable of mutation, do not exist. Sexual recombination of genes and chromosomes, on the other hand, is no absolute requisite in processes of evolution but speeds them up immensely. Mutants, hybrids and segregates are continually subjected to selective forces acting in Nature, leading to the elimination, preservation or accumulation of individual biotypes or groups of biotypes (populations), and to the formation of races (ecotypes in the terminology of TURESSON, 1922), species of different kinds and, finally, to separate phyla.

The reproduction modes are influenced by various selective forces, which act on the population structure of a species. Processes of such kind are specially evident in domesticated plant species.

The following principles are employed in contemporary plant breeding: (1) *selection*, the basic principle in all types of crop plant improvement, (2) *hybridization and segregation*, involving F_1 heterosis, gene recombination and back-crossing, (3) *doubling* or other *increases* in chromosome number (in some cases also *decreases* in chromosome number), (4) *changes of chromosome structure* (among them inversions, translocations and transpositions used in so-called chromosome engineering or surgery) (5) *gene mutation*, and, finally, (6) *the utilization of extranuclear* (cytoplasmic) *inheritance*. Principle (3) comprises phenomena of polyploidy, diploidy, aneuploidy and haploidy. Principles (4) and (5) are here kept separate from one another. Possibly they are related to changes in different constituents of the chromosomes (protein links *versus* DNA). At least in diploid and diploidized crop plants, the two groups of changes are distinguished by definite differences in viability behaviour.

2. Modes of reproduction

In the following survey attention is especially paid to agricultural plants, although some data on ornamentals, horticultural species and forest trees will also be included. In his Manual of cultivated plants BAILEY (1924, 1951) enumerated about 5,000 phanerogams, representing 1,500 genera and 194 families. A number of semi-domesticated or semi-wild species were included. In his list of cultivated species MANSFELD (1959) counted 1,430 phanerogams. Ornamentals, officinal plants, hedge or shade trees were not listed. In comparison with these comprehensive surveys only a small number of plant species will be discussed here. Further data are found in the comprehensive monograph on cultivated plants published by ZHUKOVSKY (1964).

With regard to the different modes of reproduction ("breeding systems") the following division may be adopted (*v.* GUSTAFSSON and NYGREN, 1956):

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I. Sexual self-fertile species (mostly hermaphroditic)

Examples: *Avena*, *Triticum*, *Hordeum* and *Oryza* species, *Sorghum vulgare*, *Festuca gigantea* (JENKIN, 1959), *Pisum sativum*, *Trifolium subterraneum*, *Arachis hypogaea*, *Phaseolus vulgaris*, *Glycine max*, *Lupinus angustifolius* and *albus* (with a good deal of outcrossing), *Vicia faba* (also outcrossing), *Linum usitatissimum*, *Lycopersicon esculentum*, *Nicotiana tabacum*, *Lactuca sativa*, as well as numerous annual ornamentals. *Picea omorika*, although monoecious, is said to be self-fertile and uniform in Nature (LANGNER, 1959; *cf.* GUSTAFSSON and MERGEN, 1964).

II. Cross-fertilizing, more or less self-sterile[1] *hermaphroditic species*

Examples: *Secale cereale*, numerous sexual perennial grass species (for instance in the genera *Lolium*, *Festuca* and *Dactylis*), *Allium cepa* and other *Allium* species, *Beta vulgaris*, *Fagopyrum esculentum*, *Sinapis alba*, *Raphanus sativus*, *Brassica campestris*, *napus* (transitional to I) and others, *Ribes* species, *Rubus idaeus*, *Prunus*, *Pyrus* and *Malus* species, *Trifolium pratense*, *hybridum*, *repens*, *Phaseolus coccineus*, *Lupinus luteus*, *perennis* and *mutabilis* (*cf.* GUSTAFSSON and GADD, 1965 a), *Medicago sativa* (also self-fertilizing), *Gossypium* species, *Daucus carota*, *Vitis vinifera*, *Carthamus tinctorius*, *Helianthus annuus*, *Taraxacum kokh-saghyz*, *Scorzonera hispanica*.

III. Monoecious species

These are in general more or less self-sterile (GODLEY 1955), although exceptions are found (for instance *Picea omorika*, *v.* under I). Examples: *Zea mays*, *Cucumis sativus*, *Cucurbita* species, numerous tree species of the genera *Betula*, *Alnus*, *Castanea*, *Juglans*, *Corylus*, *Carpinus*, *Quercus*, *Hevea*, as well as *Pinus*, *Picea* and *Abies* species.

IV. Dioecious species

Examples: *Spinacia oleracea*, *Asparagus officinalis*, *Cannabis sativa*, *Humulus lupulus*, *Salix* and *Populus* species, *Rubus ursinus*.

Dioecism is now and then replaced by hermaphroditism (*Vitis vinifera*) and by monoecism (*Cannabis sativa*), and dioecism may be combined with hermaphroditism and monoecism (*Spinacia oleracea*, also *Cannabis*).

V. Apomictic and vegetatively propagating (or propagated) species (GUSTAFSSON, 1946/47)

Examples: *Poa pratensis* and other *Poa* species, as well as other grass species, *Rubus* species (polyploid Moriferi), *Citrus* and *Opuntia* species, *Eugenia* species, *Hosta coerulea*, *Parthenium incanum* and *argentatum*, *Solanum tuberosum* (which also reproduces according to II), *Ipomoea batatas* (also reproducing according to II), also *Helianthus tuberosus*, *Armoracia rusticana*, *Manihot esculenta*, *Dioscorea* species, *Saccharum officinarum*, some *Lilium* species (propagating by bulbils), as well as numerous other ornamentals.

3. Basic number and polyploidy

The chromosomal state of a species is important in plant breeding, especially in applying modern principles of artificial polyploidy and mutation.

Diploid species (diploid numbers in brackets)

I. *Hordeum vulgare* (14), *Avena strigosa* (14), *Triticum monococcum* (14), *Pisum sativum* (14), *Vicia faba* (12), *Vicia sativa* (12, 14), *Lactuca sativa* (18), *Phaseolus vulgaris* (22), *Trifolium subterraneum* (12, 16).

II. *Secale cereale* (14), *Lolium perenne*, etc. (14), *Allium cepa*, etc. (16), *Beta vulgaris* (18), *Fagopyrum esculentum* (16), *Spinacia oleracea* (12), *Brassica nigra* (16), *Brassica oleracea* (18), *Brassica campestris* (20), *Sinapis alba* (24), *Raphanus sativus* (18), *Ribes grossularia*, *nigrum*, *rubrum* etc. (16), *Rubus idaeus* (14, also triploids and tetraploids), *Fragaria vesca* (14), *Prunus persica* (16), *Trifolium pratense* (14), *Trifolium hybridum* (16), *Phaseolus coccineus* (22), *Daucus carota* (18), *Pastinaca sativa* (22), *Gossypium herbaceum* etc. (26), *Taraxacum kokh-saghyz* (16), *Carthamus tinctorius* (24), *Scorzonera hispanica* (14).

III. *Zea mays* (20), *Cucumis sativus* (14), *Cucumis melo* (24), numerous tree species, *viz.* *Corylus avellana* (22), *Castanea sativa* (24), *Quercus* species (24), *Pinus*, *Picea* and *Abies species* (24).

IV. *Spinacia oleracea* (12), *Asparagus officinalis* (20), *Cannabis sativa* (20), *Humulus lupulus* (20).

V. *Citrus* species (18), *Eugenia* species (22, numerous species are polyploid), *Lilium bulbiferum* (24).

Probably diploid or derived diploid species

I. *Oryza sativa* etc. (24).

II. *Helianthus annuus* (34), *Pyrus* and *Malus* species (34), *Vitis vinifera* (38).

III. *Morus alba* (28), *Betula* and *Alnus* species (28), *Juglans* species (32), and other hardwood genera (see under 2:III).

IV. *Salix* and *Populus* species (38).

Polyploid and seemingly polyploid species

I. *Triticum* and *Avena* species (29 and 42), including *Triticum aestivum* and *Avena sativa*, *Arachis hypogaea* (40), *Glycine max* (40), *Linum usitatissimum* (30), *Nicotiana tabacum* (48), *Lupinus angustifolius* (40), *Lupinus albus* (50).

II. *Dactylis glomerata* (28), *Brassica napus* (38), *Trifolium repens* (32), *Medicago sativa* (32), *Prunus cerasus* (32), *Prunus domestica* (48), *Malus* cultivars (51, 68), *Gossypium hirsutum*, *barbadense* (52), *Lupinus luteus* (52) and *Lupinus perennis* (48).

III. *Cucurbita pepo* (40), *Betula pubescens* (56), *Betula papyrifera* (56, 70, 84), *Hevea brasiliensis* (36, 72?, 144?), *Morus nigra* (308).

IV. *Salix* species (76, 114), cultivars of *Populus tremula* (57, 76), *Rubus ursinus* (42-84).

V. *Poa* species (often high chromosome numbers, in *Poa pratensis* from $2n = 40$ up to more than 100), *Hosta coerulea* (60), *Rubi Moriferi* (28, 35 and above), *Eugenia jambos* (28, ca. 48, ca. 54), *Parthenium incanum* and *argentatum* (54 and above), *Solanum tuberosum* (48), *Ipomoea batatas* (90), *Helianthus tuberosus* (102), *Armoracia rusticana* (32), *Manihot esculenta* (36, 72?), *Saccharum officinarum* (high-polyploid), *Dioscorea batatas* (ca. 144).

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[1] The expressions "self-sterile" and "self-sterility" are here applied according to the definition of EAST (1940, p. 451): "self-sterility is taken to have been demonstrated, when the average realized fertility of a mixed group of plants produced by sexual reproduction is markedly reduced when effective self-fertilization is practiced". EAST puts the limit of self-fertility at 75 per cent of seed reduction, an arbitrary value, of course.

Diploid species are mostly characterized by regular meiosis with full bivalent pairing and normal pollen and eggcell formation. However, the evolution of different basic chromosome numbers has no doubt also involved the participation of chromosome translocations, inversions and transpositions of various kinds. This, in its turn, may imply that numerous individual genes, or segments of genes, occur more than twice in the diploid chromosome set and then form truly homologous duplicate genes. This leads to a sort of internal polyploid diploidy (homomery). In fact, diploid homomery (polymery) may not be rare at all.

In natural polyploids, as first pointed out by Müntzing (1936), a full distinction between allo- and autopolyploidy is not possible, since all allo-(and amphi)ploids are also to a great extent autoploid, *i.e.* numerous genes and gene segments occur in unchanged form three, four or more times. Mac Key (1967) has pointed out that analogous to the F_1 heterosis of diploid species (AaBbCc...) there may in polyploid species, for instance in hexaploid wheat with its three kinds of genome, exist a sort of genomatic heterosis, implying that different alleles of a gene locus occur in the simple homozygous state in different chromosome sets: $A_1A_1a_2a_2a_3a_3$, or $A_1A_1a_2a_2,A_3A_3$, etc. This may lead to heterotic vigour also under seemingly homozygous conditions. In cross-fertilizing polyploids heterosis may be brought about by regular heterozygosity also within genomes (for instance $A_1a_1A_2A_2A_3a_3$).

4. Modes of reproduction in relation to population structure

First of all it has to be pointed out that there are numerous transitions between the five reproduction types briefly outlined in chapter 2.

Between pronounced self-fertility (self-compatibility) and complete self-sterility (self-incompatibility) there is no sharp limit in hermaphroditic plant species. Complete self-fertilization does not occur in any self-fertile species. Some wild species, for instance in *Viola* and *Lamium*, are characterized by so-called cleistogamy, *i.e.* the flowers remain closed. Also in such species outcrossing takes place now and then, often by means of less expressed cleistogamy, or by means of chasmogamy (open-flowering). Numerous crop plants, recorded as normally selfing, are in fact more or less openflowering. This leads to hybrid formation and, later on, to segregation. Environmental conditions often determine the degree of „vicinism" (outcrossing). Examples are given for lupine, peanut, oat and rice species by Gustafsson and Gadd (1965 a, c, d; 1966). In tetraploid peanuts (*Arachis hypogaea*) outcrossing can reach values of 10 to 20 per cent. In hexaploid oats outcrossing has varied from nil up to 10 per cent, being especially conspicuous when high temperatures set in abruptly, shortly before anthesis. For *sativa* rice corresponding values up to 15 or 20 per cent have been found, especially in Asiatic countries. In U.S.A. the values ranged between nil and 3 per cent. Outcrossing here largely depends on the weather conditions (temperature and humidity) and the distance to foreign varieties. So-called glutinous strains were found easily to contaminate varieties in their vicinity.

Special marker genes are generally used to determine the degree of „vicinism". Such a gene is the glutinous gene just mentioned. Hammons (1964) studied the conditions of outcrossing in peanuts, using the dominant gene "Krinkle" as a marker. In nine cultivars tested outcrossing varied between 0.7 and 2.6 per cent. Such marker genes can also be used in normally *cross-fertilizing* species to determine the degree of spontaneous selfing. In *Sinapis alba* Olsson (1960) used three X-ray induced mutants, differing from normality by simple recessive genes. Cross fertilization, within *Sinapis* populations, is generally quite high, practically 100 per cent. Enforced selfing gives a low seed set; only about 3 per cent of ovules develop into seeds. However, conspicuous differences are found between plants of the same population with regard to selfing ability and inbreeding degeneration. In rape (*Brassica napus* var. *oleifera*), partially tested with the help of variations in petal colour, outcrossing covered one third and selfing two thirds of the seed set. The vicinism in small field plots amounted to about 20 per cent. Rape populations are regarded to be more or less self-fertile, with little or no inbreeding degeneration after selfing, but vicinism is nevertheless quite high under certain condition. Brown mustard (*Brassica juncea*), like rape an amphidiploid, seems to behave in a similar way. The diploid species of turnip rape (*Brassica campestris* var. *oleifera*) and black mustard (*Brassica nigra*) react in very much the same way as white mustard.

Cross-fertilizing species often possess mechanisms which facilitate wind or animal pollination (anemogamy and zoidiogamy) sometimes even preventing self-fertilization. Self-sterility (or self-incompatibility) can be viewed from various aspects with regard to mechanical hindrances to selfing in flower morphology (distylism in *Primula* or tristylism in *Lythrum*, as already discussed by Darwin, 1877) or in physiological and genetical interactions between pollen tubes and style tissue, leading to complex systems of incompatibility (*v.* Lewis, 1954; Lundqvist, 1962). In spite of these obstacles spontaneous or artificial selfing can be brought about in most hermaphroditic and monoecious species, leading to considerable variations in seed set and inbreeding degeneration. *Cf.* here, for instance, the contrast between maize and rye, or sugar beet. In *Pinus*, *Picea*, *Pseudotsuga* and other conifers, according to Dogra (1967), pollen germination and pollen tube growth is more or less normal after selfing, but a high rate of embryo mortality leads to seed sterility. Also in conifers, according to Swedish experiences, the results after artificial selfing differ from species to species, and from biotype to biotype. Some individuals are easily selfed (Ehrenberg, 1963), others give very small progeny after selfing, while some others give no progeny at all. The degree of inbreeding degeneration also differs from case to case.

In fact, the possibility of selfing, and the utilization of inbred lines in hybridization, has led to outstanding results in the improvement of many cross-fertilizing species. Geneticists now turn to the self-fertilizing species, changing them to cross-fertilizers, in order to produce hybrid F_1 varieties. Fascinating problems are involved.

Continuous plant breeding, starting long before the Mendelian era, has, as emphasized above, switched the mode of reproduction of a species from one breeding system to another, although the limits between the types of reproduction have never been profound. This is not only so with regard to self- and cross-fertilizing species in the case of hermaphroditism. Mutual changes are also possible with regard to monoecism, or/and dioecism, and hermaphroditism. Examples: *Cannabis sativa*, hemp, is normally dioecious, with conspicuous differences between the male and female individuals in morphology and productivity. Rational harvesting is difficult owing to the different time of the two sexes. Fiber yield in dioecious hemp consists to 70 per cent of female and to 30 per cent of male origin (HOFFMANN 1961). The fresh yield is even more displaced to the female side (up to 80 per cent). Due to this and other reasons dioecism has been intentionally switched over to monoecism (and hermaphroditism). The change in population structure can be illustrated by the following sex proportions in a breeding program from 1941 to 1948 (HUHNKE *et al.*, 1950):

	Males	Males femalelike	Monoecious individuals	Females
1941	15.4%		50.2%	34.4%
1948	0.01%	0.02%	98.4%	1.5%

The breeding of high-productive monoecious hemp has been successful in many countries: Germany, Soviet Union, Sweden, Hungary, France, also U.S.A.

Most cultivars of *Vitis vinifera* are hermaphroditic and self-fertile. Cytologically seen, the hermaphroditic individuals are males (XY), since numerous females and single males arise in their selfed progenies. Wild species of *Vitis* are dioecious. The females are pollen sterile hermaphrodites (HUSFELD, 1962). *Spinacia oleracea* is generally considered to be dioecious, but in most cultivars there also occur hermaphroditic individuals, which in addition to male or/and female flowers also possess hermaphroditic ones. Male plants are inferior to the females in productivity. Breeding programs, therefore, also include the production of hybrid populations consisting of purely female individuals.

In this connection a note may be added about conifers. It is well-known since long ago that the degree of monoecism is quite variable in some species; single individuals are predominantly male, others predominantly female. Numerous variations as to flowering have been found in Nature and in experiments and many are now propagated by grafting. A fully developed dioecism may under certain conditions, as for instance intercrossing in seed orchards, be helpful for the establishment of hybrid vigour.

Finally, a brief discussion may be added with regard to apomixis and vegetative propagation. Apomixis in its strict sense simply means reproduction without „mixis", *i.e.* without sexual seed formation. Apomixis may be divided into two groups: (1) *Agamospermy*, which is the formation of seed by asexual processes. It consists of (i) apospory or diplospory followed by parthenogenesis, or of (ii) adventitious embryony. In (i), gametophytes with an unreduced chromosome number are formed, and eggcells develop into embryos without fertilization. Examples: *Rubi Moriferi* (blackberries), *Poa* species and other grasses, *Parthenium* species, *Rudbeckia* species. In (ii) diploid cells of sporophyte ovules give rise directly to embryos and seeds develop. Examples: *Citrus, Eugenia, Hosta, Opuntia, Alnus, Sarcococca.* (2) *Vegetative propagation*, with no seed formation, implies that vegetative parts (bulbs, bulbils, stolons, root and stem parts) take over the survival and spread of a biotype or a species. In numerous phanerogams vegetative propagation is a means of dispersal in addition to the formation of functioning seeds. In others, it may replace seed formation, partially or entirely. "Vivipary" (or "biotechnosis") is a rather common feature in grass species; it implies the formation of bulbils in the inflorescence: the bulbils often germinate into new seedlings already when remaining in the inflorescences. Details of the subject are found in articles by GUSTAFSSON (1946/47) and GUSTAFSSON and NYGREN (1956).

In the case of agamospermy many deviations appear. Parthenogenesis may occur also in chromosome-reduced ("haploid") embryosacs. In some cases haploid parthenogenesis has been found in normally sexual species, for instance in *Zea mays*, *Secale cereale*, *Hordeum vulgare*, or in tetraploid *Solanum tuberosum*, with its pronounced vegetative dispersal, or in polyploid apomictic species as in *Poa pratensis* and *alpina*. Other deviations imply that unreduced eggcells give rise to (poly) triploid and (poly) tetraploid individuals after fertilization. This occurs rarely in normally sexual species, more commonly in some aposporous and diplosporous species. In an agamospermous plant species, for instance in *Poa pratensis* with, say, 2n = 70 chromosomes, the offspring may in principle consist of (1) individuals having exactly 2n = 70, arisen from unreduced eggcells after parthenogenesis, (2) individuals with chromosome numbers varying around 2n = 70, which are the results of fertilization of eggcells in reduced gametophytes, (3) individuals with chromosome numbers around 2n = 105, resulting from the fertilization of unreduced eggcells ("70 + 35"), (4) individuals with 2n = 140, arisen from the fertilization of unreduced eggcells with unreduced sperm nuclei (70 + 70), (5) individuals with 2n = 35, arisen after (poly) haploid parthenogenesis. Types (1) and (2) are most frequent, their mutual ratio depending on the choice of parental biotypes. Type (3) occurs more or less rarely. Types (4) and (5) are of sporadic occurrence.

Another variation of agamospermy is found in pseudogamy. Genera of the families *Rosaceae* and *Gramineae* (as well as other families) need pollination, but no fertilization of the eggcell is necessary. Embryo formation is an autonomous process. However, for the development of endosperm the central nucleus of the embryosac (two fused polar nuclei) must be fertilized. Among cultivated plants blackberries (*Rubi Moriferi*) and *Poa* species behave in this way. Some ornamentals also belong here.

In numerous phanerogams normal sexuality is combined with methods of vegetative propagation. This leads to interesting evolutionary consequences. The often-discussed phenomenon of "genetic drift" or the "Sewall Wright effect", implies the chance loss or increase of rare genes in subsequent generations. It lacks significance, however, in species propagating vegetatively, sexual or apomictic. On the other hand, vegetative propagation facilitates plant breeding immensely, since any desired biotype (or group of biotypes), reproducing also vegetatively, is easily mass-propagated. Artificial means of mass-propagation consists of grafting, budding, rooting of cuttings, division of tufts, etc., in addition to the natural means of stolon, tuber, bulb and bulbil formation, all highly developed methods in horticulture, forestry and gardening. Clone multiplication is also possible in annual species, for instance in rye. By such vegetative methods individual biotypes can be clone tested on a large scale and mutually compared with regard to vegetative and generative properties and genotype-milieu interactions. Seed orchards in conifers and polycrosses in fodder plants (alfalfa, grasses) are built up on principles of clone propagation, selection and intercrossing, combined with progeny testing.

Species like potatoe, sweet potatoe, topinambur (*Solanum tuberosum, Ipomoea batatas, Helianthus tuberosus*) combine vegetative propagation with a series of transitions from full seed fertility to full seed sterility. Horse radish (*Armoracia rusticana*) very rarely produces fertile seed.

5. Modes of reproduction in relation to plant breeding

Such problems have partially been touched upon in the preceding chapters. A few additional notes may be desirable.

Already before the turn of the century it was found that self-fertilizing crop plants (barley, oats, peas and wheat) consist of heterogeneous mixtures of different lines (so-called "land varieties"), and that a selection within these mixtures often lead to remarkable and almost instantaneous improvements. Individual lines surpassed the mixtures in yielding ability, lodging resistance, disease resistance, quality properties etc. "With the help of this separate breeding or predigree culture we succeeded to isolate races, which in every detail kept the characteristics, after which the parent had been selected, so far as those were *real* botanical characters of some value in systematic respects, and kept them with a uniformity never before observed by us" (NILSSON, 1896, pp. 125-126, translated). This meant "a complete change of the earlier working methods". The use of the previous selection methods was no longer "to produce and to fix such properties in the crop plants, which were of value in the farmer's practice, but rather to recognize and to control the uniformity of the valuable properties". It was also found, through this Svalöf work, that selection within a line mixture soon came to an end and that repeated selection within individual lines gave no further result. The successful theoretical interpretation came with the pure line concept and the formulation of the expressions genotype-phenotype by JOHANNSEN (1903, 1909).

Every careful breeder, working with self-fertilizing cereal species, knows the limitation of the behaviour of pure lines in practice. A completely homozygous strain is intermixed, sooner or later, with foreign seed material. It gives successively rise to mutations in major and minor characteristics. In addition, outcrossings will in certain years and under certain conditions lead to hybridization and subsequent segregation, with new line mixtures as a consequence (for discussions of the degree of outcrossing, *v.* the preceding chapter). WÖHRMANN (1967) has recently pointed out this fact and stressed the significance of outcrossings in plant breeding. He also advocates the view that heterozygotes are often superior to their respective homozygotes, and that also self-fertilizers should be handled in plant breeding as populations. In fact, this view is already partially realized, since many cultivars of cereal species consist of mixtures of similar homozygotes instead of single homozygotes. This is made in order to secure varietal adaptability combining it with a fair degree of uniformity. The isolation of pure lines from originally heterogeneous or hybrid populations is an easy task in self-fertilizing species, the heterogeneity of a variety depending on the strictness of the preceding selection and elimination.

In lupine species SENGBUSCH (and others) has utilized the spontaneous occurrence of rare genes or mutations to adapt the species to agricultural needs. He mass-reproduced, in few generations, original small populations of *Lupinus angustifolius, albus* and *luteus* and was able, by simple but precise methods of screening, to select individuals with the desired characteristics, for instance low alkaloid content. This "Sengbusch method of breeding" (GUSTAFSSON and GADD, 1965 a) can no doubt be elaborated and used in other crop plants, especially in cases where some remaining heterozygositiy is left, if enough seed is mutagenically treated, and furthermore of course, in segregating and back-crossed materials of appropriate hybrid offspring. Some types of disease resistance can be induced by mutation and detected in segregating progenies after mass-infection in greenhouse cultures.

With NILSSON-EHLE's analysis of gene recombination and polymery (the occurrence of "gleichsinnige Faktoren"; 1909, 1915) the theory of plant breeding was further developed. It may be remembered in this connection that MENDEL himself pointed out similar methods of plant improvement in his „Versuche über Pflanzenhybriden" and especially in his letters to NÄGELI. NILSSON-EHLE worked out ingenious schemes for gene recombination and transgression. The latter principle is of special importance with regard to yield improvement, when genes for high yield are combined from varieties of greatly different origin (by many Soviet breeders this form of transgression is named "distant hybridization"). Properties of increased early maturity and lodging resistance often appear as transgressions in distant hybridization, combining different genes. The techniques of gene recombination were enriched by the introduction of back-crossing especially in cases where one or a few properties of special character should be transferred to a high-yielding strain lacking in some practically important feature (for instance in disease resistance).

The analysis of inbreeding degeneration in cross-fertilizing species, with subsequently restored and improved productivity in hybrids, was first carried out in maize by SHULL (1908, 1909, 1910). The double-cross technique was elaborated by JONES (1918) and refined by him and others (*v.* SPRAGUE, 1959). Maize, although monoecious, is rather easily self-fertilized. For sugar beet similar principles were worked out at the Hilleshög Institute (TJEBBES, RASMUSSON), although extreme selfing and homozygotization was difficult to carry through. In rye, which is more sensitive to selfing and inbreeding than maize (HERIBERT-NILSSON, 1926; NILSSON-EHLE, 1926), continuous selection is usually carried out and combined with progeny tests. In the case of special quality characters, open to accurate chemical analyses, not even progeny tests are necessary (TEDIN and PERSSON, 1961). Both in rye and sugar beet artificial polyploidy is of practical importance and has resulted in commercial varieties. Clonal analysis will no doubt enhance precision of selection on the diploid as well as on the tetraploid level.

In fact, vegetative propagation, clonal analysis and progeny testing are all united into a definite working scheme for the improvement of many cross-fertilizing fodder plants (grasses, alfalfa, also clovers) and conifers (pines, spruces, larches). The scheme is built up on selected clones, in general numerous ones, in order to secure sufficient genotype multitude and adaptability on high production levels when intercrossed in a poly-system (*v.* chapter 4).

Inbreeding leading to complete (or almost complete) homozygosity requires several generations of selfing. In some instances already the first or second inbreeding generation is used for hybrid production. The use of haploid embryos and seedlings, with subsequent chromosome doublings, secures directly full homozygosity (*v.* CHASE, 1952). Special methods for the discovery of haploids are now worked out in many species. Their rates can be increased by species (and genus) crossings, or by fertilization with aged or irradiated pollen. It is interesting to note that homozygous progenies, obtained from haploids, become again variable rather quickly, as is also the case in normally inbred strains (for the contrast in this respect between self- and cross-fertilizing species, *v.* GUSTAFSSON, 1961, p. 480). This indicates the origin of numerous mutations with small effects associated with alterations in the normal mode of reproduction.

The mode of reproduction greatly influences the success or failure of artificial autopolyploidy (as well as allo- and amphipolyploidy). The agricultural evaluation of the success of autoploidy in various species goes back to analyses by MÜNTZING, TURESSON and LEVAN (*cf.* LEVAN, 1945). Three chief characteristics of a plant species decide about failure or success: (1) whether the chromosome number is high or low, (2) whether the mode of reproduction is autogamy or allogamy, (3) whether the species is cultivated for seed or for vegetative matter.

The ideal combination of characteristics is at hand when the species (1) is diploid with a low basic number, (2) is allogamous, and (3) is cultivated for vegetative production only. Artificial tetraploids have performed well in red clover and alsike clover, triploids and tetraploids in sugar beet. These species are low-chromosomal (with $x = 7$, 8 and 9 respectively), greatly self-incompatible and cultivated for their vegetative mass (leaves and stems in clover; roots in sugar beet). Among seed yielding plants rye, for instance, has given excellent polyploid results. The basic number of rye is $x = 7$, and it is allogamous. The same holds true of white mustard. Barley, on the other hand, has certainly a low basic number ($x = 7$), but is autogamous and seed delivering. Its tetraploid is low-yielding. A similar contrast is noticed in *Brassica*, where tetraploid turnip rape (*Brassica campestris* var. *oleifera*), with $2n = 40$ and pronounced allogamy, produces about half diploid yield. Tetraploid rape (*Brassica napus*), with $2n = 76$ and high self-fertility, gives just 15-20 per cent of the diploid yield. Rape itself is a successful amphidiploid, arisen from crosses of *Brassica campestris* and *Brassica oleracea*. Tetraploid turnips (*Brassica campestris* var. *rapa*) are high-yielding (HAGBERG and ÅKERBERG, 1962). Inferior autoploids have been found in tetraploid soy bean and pea-nuts, which are high-chromosomal and highly autogamous. Triploid aspen, to take an example from forest trees, is high-productive. Normal aspen (*Populus tremula*) certainly has a high basic number ($x = 19$), but its chromosomes are small; furthermore it is allogamous (dioecious) and vegetatively used. Potatoe (*Solanum tuberosum*) is a polyploid, with $2n = 48$. Its autoploid, with $2n = 96$, is in spite of the use of its vegetative propagation method drastically inferior. High-productive triploid *Citrullus vulgaris* (water melon), with the basic number $x = 11$, is obtained in an allogamous species and its fruits are used. It is also seed sterile, a fortunate condition in this case. It must be produced anew, like many other triploids from crosses between diploid and tetraploid individuals within the species. In fruit trees, aspens etc., such high-productive triploids, auto- or alloploid in origin, can be mass-propagated vegetatively.

Also in the case of mutations the reproductive system exerts a great influence on the breeding methods and results. We now know that spontaneous and induced mutants can be directly used as new varieties in agriculture. (Freak mutations in ornamentals and vegetables are not dicussed here.) Examples from *Pisum*, *Hordeum*, *Oryza*, *Triticum*, *Arachis*, *Nicotiana*, *Sinapis* may be referred to. In autogamous species the homozygous mutations have to be used. There is a remarkable contrast in viability and productivity between homozygous gene mutations (in the wide sense of the term) and chromosome rearrangements (translocations and inversions). In general the proportion of high-reproductive homozygous gene mutations is rather low, their rate depending on the screening methods, gene loci mutated and the phenotypic deviation of the isolated mutants. Using special techniques the undesired changes are easily eliminated. It is, in my opinion, no great difficulty in autogamous diploid crop plants to select high-productive mutants with improved earliness, lodging resistance, disease resistance, dwarf or semi-dwarf habit etc., although, of course, it is a long way to produce and release new trade varieties. Homozygous chromosome rearrangements are in general high-productive; around half of them reach the production level of the parent variety in a species like barley. The rearrangements are often associated with minor phenotypic changes (in some instances probably depending on position effects). The use of chromosome rearrangements will no doubt increase in the future, also in combination with so-called chromosome engineering (surgery), *i.e.* the transfer of beneficial properties by segment transposition from one variety or species to another (SEARS, 1956), or with the planned production of duplications within varieties (HAGBERG, 1966).

The "Sengbusch method" of breeding referred to above (p. 112) is quite useful in many species with high heterozygosity. The mass-reproduction of a population into millions and millions of individuals accompanied by the development of *precise screening techniques* will often lead to the discovery of single individuals having the desired property. These may then be utilized directly as new varieties, or after out- or back-crossings to other valuable types. It must not be forgotten that the present day plant breeding of important crop plants uses enormously high numbers of individuals. Now and then successful "recombinants or segregates" may actually have resulted from rare mutations.

In autogamous polyploids, as in wheat, and oats, the induction of gene mutations with no concomitant chromosome rearrangement may be advantageous. This is easily performed, since some chemical mutagens preferably induce gene mutations. Chromosome rearrangements often give rise to aneuploids, segment duplications and deficiencies greatly decreasing viability. The problem of homozygous genome heterosis (MAC KEY, *v. p.* 110) has to be considered here (for instance A_1A_1, $A_2A_2 < A_1A_1$, $a_2a_2 > a_1a_1$, a_1a_2).

Spontaneous or induced mutations have quite a different implication in cross-fertilizing species. Mutations which decrease viability when homozygous often do not affect viability at all when heterozygous, or if they do, they may fall within the range of a slight decrease or a slight increase of viability (95 to 105%). On the other hand, heterozygotes of major mutations often show small quantitative changes. The reaction system of viability (race- or genecology of TURESSON, 1923) has also to be considered in this connection. It implies that genotype-milieu interactions of pure lines, or mixtures of pure lines, and population-milieu interactions in allogamous species never are quite static. Genotype survival, competition, inferiority and superiority depend on complex exterior and interior conditions, abiotic and biotic (*v.* GUSTAFSSON, 1954, pp. 606-616, for a discussion on these points). It is therefore a fundamental mistake to draw the general conclusion that viability-decreasing, or viability-increasing mutations, always act as such, in the homozygous or/and the heterozygous state.

Here the behaviour of Mari barley, arisen as mutation, may be referred to. It is rather widely cultivated owing to its increased earliness and high lodging resistance. Under extreme long-day conditions in the phytotron (24 hours of light) it is inferior to its parent variety in vegetative as well as in generative properties. It is, however, equal or definitely superior under moderate long-day and short-day conditions (16 and 8 hours of light). It also has a wider temperature tolerance (DORMLING *et al.*, 1966). Consequently, a mutation detrimental in certain environments, is beneficial in others. This is valid with regard to numerous homozygous mutations, as exemplified here by Mari barley, but most definitely also in the case of heterozygous mutations. In fact, ecotype formation in nature is based on such population-milieu interactions.

When irradiated, or treated mutagenically in other ways, cross-fertilizing populations become more variable, especially when the original population heterogeneity is not very large. A the same time they may obtain a greater climatic adaptability. An example of such an increase in population variability is afforded by the X-rayed diploid white mustard (*Sinapis alba*), from which the variety Svalöf's Primex was selected and released (ANDERSSON and OLSSON, 1954). Modern biochemical methods of oil, protein and amino acid determination, also in the case of intact living seeds, should be able to make selection pressure much more precise. Screening in species like rye, maize, sun-flower etc. should become sharper and more effective by such methods.

Mutations in vegetatively propagated plants are more difficult to handle, since chimeras ("histomutants") usually arise. The chimerical constitution itself may often be advantageous from a viability point of view. In fact, it has been discussed to produce new types of histo-mutants for instance in *Solanum tuberosum*. It was indicated in the work done by HEIKEN (1958, 1960) and others that mutants may be of direct importance. In vegetatively propagated ornamentals chimeras are quite common. Special techniques have been developed to give rise to or, on the contrary, to unmask chimeric situations. (Here reference is made to the proceedings of the Fourth Series of Erwin Baur Memorial Lectures, Gatersleben 1966, Editor HANS STUBBE.)

A few words are necessary on the question of extranuclear inheritance, since this has become an important tool in plant breeding, especially with regard to cytoplasmically controlled male sterility in cross-fertilizing species (maize, *Sorghum*, sugar beet, *Allium cepa*). Cytoplasmic male sterility (CMS) may be counteracted, entirely or partially, by pollen restoring nuclear genes. The male sterile condition may be kept cytoplasmic from generation to generation, transmitted *via* the eggcells of male sterile plants and applying pollen from lines lacking in pollen restoring genes. CMS is overcome by the use of pollen parents having such genes. An interesting development of the last few years involves planned changes of autogamous into allogamous species, for instance introducing CMS to hexaploid *Triticum aestivum* from diploid *Aegilops caudata*, tetraploid *A. ovata*, or tetraploid *Triticum timopheevi* (KIHARA, 1967). Another method, with the same goal but resting on the action of nuclear genes, has recently been proposed in barley (HAGBERG, 1966), *viz.* the combining of genes for male sterility and DDT-resistance in chromosome 7 to closer linkage.

There is still considerable dispute about the mode of origin of extranuclear inheritance. A certain autonomy seems plausible, especially when definite cytoplasmic organelles and structures are involved, for instance plastids and mitochondria. In some cases, at least, mutations in nuclear genes have led to extranuclear inheritance, which can then be freed from the presence of these nuclear mutations. The possibility of a direct induction of extranuclear mutations for male sterility is controversial, although FAVRET and RYAN (1966) described such mutants in barley.

6. Modes of reproduction in relation to plant exploration

Plant explorations comprise the collecting of disseminules (seeds) in sexual species and propagules in vegetatively reproducing species. The procedures of collection are in a way self-evident. Seeds can often be stored for a long time, although cases are known, for instance in *Populus* and *Salix*, where they must be sown shortly after maturity. Dry dormant propagules can similarly be stored with adequate handling and then, later on, be sown, grafted or budded. Runners, layers, scion materials in active growth have in general to be used immediately. Pollen of several tree species can be stored for a year or more and be sent for pollination purposes the world over.

Many cultivated plant species have been utilized outside their natural area of distribution, and numerous species of crop plants, fruit trees, vegetables and ornamentals are more or less cosmopolitan since long ago. Others are recent introductions to new areas of cultivation. Well-known examples are *Trifolium subterraneum* and *Lupinus* species, *Pinus radiata* and other conifers, *Eucalyptus* species, etc. In the case of disease resistance the use of primitive populations in back-crossing work (and chromosome surgery, SEARS) often give outstanding results. Similarly with regard to extranuclear male sterility, which can be transferred from primitive wild species and varieties to high-bred cultivars. Dwarf and semidwarf materials may become of value in certain regions, for instance in fertile regions with high humidity. Other valuable properties are drought resistance and deviations in fatty acid, protein content, or amino acid constitution, loss of alkaloids, etc. Natural populations, as well as recent mutant assortments, have to be analysed for valuable characters and then kept in the best way possible. Improvements in storage methods are necessary for all kinds of material.

A few words, finally, about the sample size of seeds and propagules in relation to different modes of reproduction. In pure lines a couple of seeds suffice for further mass multiplication. Primitive populations of autogamous plants consist of line mixtures. This condition ought to be kept in mind so that a fair representation of the multitude is obtained already in the original collection work.

In cross-fertilizing species the valuable genes are often in a heterozygous state. Dominant properties are generally easy to handle. Recessive genes are more difficult to register and to preserve. Often, in the homozygous condition, they are responsible for valuable characters. In consequence, population size should be kept rather wide. Nevertheless, many genes potentially important for further domestication will be lost also in the case of extensive field collections and subsequent mass reproduction (according to the SENGBUSCH method). Then methods of artificial mutagenesis have to be applied.

Parthenogenetic and other apomictic species behave like autogamous plants with regard to collection procedures. In the case of extinct sexuality a few seeds are enough. Mixtures of apomicts should be treated as mixtures of pure lines. Different apomicts of a species are often easy to distinguish, both with regard to qualitative and quantitative properties. The genotype multitude is then readily determined already in the field.

In the case of vegetatively propagated materials, finally, (also including fruit and forest trees), the originally wild or semi-wild populations should be kept as multiform as possible in special archives of clones and populations. In forestry, with its rapid development of "seed orchards", built up on selected plus and élite trees, plant breeders must be aware of the fact that it is a most necessary task to preserve a *wide variability* for the case of future selection work. National parks of forests, resting on natural regeneration, have to be additional collection areas for plant breeding in years to come. However to preserve wide assortments of genes, chromosomes and cytoplasms, and to enrich them further, are important objects in all kinds of cultivated species.

7. Concluding remark

Here, finally — although outside the scope of this article — the exploration work begun by Soviet scientists guided by the spirit of VAVILOV and ZHUKOVSKY (*cf.* VAVILOV, 1926; ZHUKOVSKY, 1964) must be referred to. After it started almost five decades ago this exploration work has been combined with studies of systematics, genecology and cytogenetics. The fact was established by the scientists mentioned, and amply corroborated by other scientists, that the exploration of wild and semi-wild relatives of cultivated plants is a highly important principle in plant breeding and evolutionary biology. To this factual case the need of a precise and well-performed world program should be accentuated for the further enrichment of variability by means of induced mutations: on the gene, chromosome and cytoplasm levels. The preservation of *old* genes and genotypes and the induction of *new* genes and genotypes, and their use in continued hybridization and gene recombination, complete each other. Neither method is obsolete or unnecessary. Both help to increase the resources of crop plant improvement.

Zusammenfassung

Es werden die verschiedenen Formen der Fortpflanzung bei Kulturpflanzen behandelt, wie Auto- und Allogamie bei geschlechtlicher Vermehrung, einschließlich Selbstfertilität und Selbststerilität, und die verschiedenen Möglichkeiten der vegetativen Vermehrung und Apomixis. In Verbindung mit dem Ploidiegrad und der Chromosomengrundzahl haben die verschiedenen Fortpflanzungsformen einen erheblichen Einfluß auf die Populationsstruktur und auf den Erfolg oder Mißerfolg der einzelnen in der Pflanzenzüchtung angewandten Methoden. Das gilt für die Anwendung von Selektion, F_1-Heterosis und Genrekombination ebenso wie für Polyploidie und induzierte oder spontane Mutation. Es wird betont, daß die plasmatische Vererbung, auch im Falle von Polyploidie und Mutation, nicht außer acht gelassen werden sollte.

Zwischen Auto- und Allogamie sind Übergangsstadien vorhanden. Autogamie ist in keinem Fall oder wenigstens in sehr wenigen Fällen obligatorisch. Bei allogamen Species sind Inzucht und nachfolgende Kreuzung wesentliche Möglichkeiten für eine Leistungssteigerung durch Züchtung. Bei diözischen, monözischen und hermaphroditen Species kann die

Fortpflanzungsform durch geeignete Methoden der Genrekombination, Mutation und Selektion geändert werden. Apomiktische Species, z. B. verschiedene Gräser, zeigen Übergänge zwischen mehr oder weniger obligatorischer Apomixis (Parthenogenesis und Viviparie) und teilweiser oder völliger Sexualität.

Am Schluß der Arbeit werden Beispiele gebracht, wie die verschiedenen Fortpflanzungsformen die Methoden beeinflussen, die bei der Erforschung und Erhaltung der pflanzlichen Gen-Pools angewendet werden.

Schließlich wird die Pionierarbeit von Vavilov, Zhukovsky und ihren Mitarbeitern gewürdigt.

Günstige Gene, Chromosomen und Cytoplasmen, die in natürlichen Populationen vorhanden sind, müssen erhalten bleiben. Neue günstige Gene usw. sollten laufend durch Mutation geschaffen werden. Die Erhaltung der alten Gene und die Induktion neuer sind Hilfsquellen für den Züchter in seinem Bemühen um fortgesetzte Leistungssteigerung der Kulturpflanzen.

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