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SOME FUNDAMENTAL CONSIDERATIONS ON INTERSPECIFIC HYBRIDIZATION

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ABSTRACT. It is shown that the extent to which wild species and primitive forms are utilized in crop breeding depends on the nature of the crop and on the availability and accessibility of the species. Useful genes derived from related species are predominantly those for resistance to diseases and insects, but adaptability, quality traits, and yield also could be improved by including wild species and primitive forms in breeding. Some special applications are the induction of haploids, (re)synthesis of allopolyploids and induction of cytoplasmic male sterility.

Gene transfer is usually brought about through normal recombination, but, in cereals, induced recombination and translocation have also been applied. It is emphasized that the normal recombination is most effective. This implies that species that are closely related to crop plants are to be preferred. The breeder should resort to remote species only if they carry unique genes not available in more closely related species.

The concept of prebreeding within wild and primitive species before crossing with cultivated forms is explained along with the concept of column breeding for polygenic traits. An integrated breeding procedure based on these concepts is presented. The concepts, though basically correct, need to be critically evaluated as to their practicability in breeding.

Pre- and postzygotic barriers to interspecific hybridization are listed along with ways to overcome them. Evolutionary and genetic aspects of interspecific barriers are discussed and data presented on the genetic control of crossability of species. Some experimental data in *Solanum* and grass species clearly illustrate the nature and extent of various interspecific barriers in remote hybridization.

Index Descriptors: interspecific hybridization, crossability, prebreeding, column breeding, interspecific barriers, *Solanum*, grasses, and introgression.

RATIONALE FOR INCLUDING WILD SPECIES IN BREEDING

During their evolution, wild species have survived selection pressures from various diseases, pests, and adverse environmental conditions. This, in addition to the tremendous differences in soil, water supply, temperature, daylength, and light quality and quantity in the centers of diversity, has given rise to the characteristic wealth of resistances and other genetic variation. On the other hand, cultivated forms are relatively young and protected by man, so their genetic variation is usually restricted. They are vulnerable to various adverse factors, as several calamities in history have shown. Logically, plant breeding has to rely upon the treasures in the gene centers.

Some fifty years ago, plant breeders were not yet prepared to utilize wild species for crop improvement. At present, breeders' minds have changed, and both wild and primitively cultivated material from the gene centers are

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being utilized in many crops. The extent to which related species are used depends on the nature of the crops and the availability and accessibility of related species.

In crops like barley (*Hordeum vulgare*), corn (*Zea mays*), field bean (*Phaseolus vulgare*), and cassava (*Manihot utilissima*), most useful variation is available in the crop itself and interspecific hybridization is not readily applied (Hawkes, 1977). In ornamentals, clovers, grasses, and fruits, the distance between cultivated forms and wild species is so small that including wild species in breeding is obvious. Quite a few crops have escaped extinction by using wild relatives: potato (*Solanum tuberosum*) in Europe (late blight), sugar cane (*Saccharum officinarum*) (mosaic virus), coffee (*Coffea arabica*) (rust disease), and tobacco (*Nicotiana tabacum*) (tobacco mosaic virus and bacterial wilt). A different use is being made in crops that usually are grafted onto wild root stocks, like citrus (*Citrus* spp.), rubber (*Hevea* spp.), grape (*Vitis vinifera*), roses (*Rosa* spp.), and fruit trees, the wild species being resistant to soil-borne diseases. Most extensive has been the systematic introgression of desirable genes from wild material through crosses and backcrosses under selection in each generation. So far, desirable genes from wild and primitive forms have been predominantly those for race-specific and polygenic resistance, tolerance, and immunity. Genes for increased adaptability of crops have extended the areas where these crops can be grown, e.g., wheat (*Triticum aestivum*), rye (*Secale cereale*), and grape (*Vitis vinifera*). An up-to-date example of increased adaptability are some wild *Lycopersicon* species as sources of genes leading to greenhouse-grown cultivars of tomatoes that need less energy (Institute of Horticultural Plant Breeding, Wageningen). Also, quality characters have been improved by using wild species in breeding cotton (*Gossypium hirsutum*) (fiber quality); potato (*Solanum tuberosum*) (texture and protein content); rice (*Oryza sativa*), oats (*Avena sativa*) and soya (*Glycine max*) (protein content); tobacco (*Nicotiana tabacum*) (lower nicotine content); strawberry (*Fragaria ananassa*), and tea (*Camellia sinensis*) (improved flavor). Unexpected yield increases have been obtained in hybrid progeny from oats and *Avena sterilis* (Takeda and Frey, 1977); potato and *Solanum vernei, S. goniocalyx*, and *S. demissum* (Huijsman and Wiersema, unpublished results); and strawberry with its ancestral species *Fragaria chiloensis* and *F. virginiana* (Evans, 1977). Such effects on polygenic characters may be due to interactions between genes from wild and cultivated species. New flower shapes and colors, thornless *Ribes*, and branched ears in wheat and rye are other surprises from nature.

Since the early and mid-sixties, large-scale breeding programs, aimed at broadening the genetic base of potato breeding, have been carried out using primitive and wild potato species from South America. These species produce normal tuber yields under short-day conditions only. Repeated cycles of positive mass selection for tuber production under long-day conditions in

Europe and the United States have yielded genotypes producing considerably higher tuber yields than the initial material. Crosses between these adapted genotypes and S. *tuberosum* cultivars often displayed heterosis and have yielded new cultivars. In addition, a considerable number of resistance genes have been obtained this way (Simmonds, 1966; Plaisted, 1972; Haynes, 1972; Glendinning, 1979; and Maris, unpubl. results).

Some more sophisticated applications of wild and primitive species are the induction of haploids, (re)synthesis of allopolyploids, induction of cytoplasmic male sterility, analytic breeding, and increasing knowledge in the evolution of cultivated species.

When there is sufficient affinity between related species and cultivated crops, crossing and backcrossing is the most obvious and efficient way of introducing desirable genes through normal recombination. The increasing knowledge of genetic control of pairing behavior in *Triticinae* (Sears, 1976) offered tools for gene transfer through induced recombination. Where even this technique failed, the induction of translocations by irradiation of alien addition lines has successfully been applied (Sears, 1956; and others).

When initiating a program of utilizing wild species in breeding, the first step is to collect as many accessions as possible of related species and genera either from existing gene banks or through expeditions in the centers of diversity. The material collected should be taxonomically identified, catalogued, and properly propagated and stored. The affinity between species and crops has to be determined either through taxonomic (Anderson, 1949), biochemical (Johnson et al., 1967), cytological (Kihara, 1930), or genetic methods (Gerstel and Phillips, 1958) or combinations of these methods. Species with the greatest affinity to the crop can be used most efficiently for gene transfer.

Most important is the systematic evaluation of species for desirable characters followed by pre-breeding, as will be explained below. A good knowledge of barriers between species and of methods to overcome them is indispensable. This will be explained in more detail along with some fundamental aspects. It will also be illustrated with some results from relevant investigations.

THE CONCEPT OF PREBREEDING PLANT SPECIES

Plant species are separated by barriers to intercrossing. This prevents them from being submerged in one large gene pool. A breeder has to break or circumvent these barriers in order to make the genes accessible. Wild species and cultivated crops may be remotely related. In such cases, the breeder may have to use bridging species when direct crosses with cultivars do not succeed. Even when the direct crosses are successful, several backcrosses may be needed to nobilize the hybrids. Both the use of bridging species and backcrossing are laborious and usually lead to a decreased level of desirable polygenic traits. Species that are closely related to the cultivated crop are to be preferred.

Furthermore, the nobilization process is speeded up at the diploid level, because at the polyploid level, undesirable "wild genes" will disappear more slowly from the population.

Prebreeding is a procedure which may promote the efficiency of interspecific hybridization. It is called prebreeding because it implies breeding within each species before crosses with cultivated material are made. Prebreeding, in addition to selection for adaptation to the prevailing environmental conditions, may include: (1) a thorough evaluation of desired characters within the species before crossing with cultivars, (2) a study on the genetics of such characters within the wild species in order to avoid erratic genetic ratios due to unbalance in interspecific hybrids, (3) concentrating genes controlling polygenic traits, and (4) combining within the species different valuable characters, which usually are scattered over different accessions of that species.

The results of a prebreeding program may be highly valuable genotypes that are environmentally adapted and that comprise concentrated genotypes for the required characters. A clarification of the genetics of these characters may have occurred. Especially, crosses between a crop and remotely related species should not be carried out before the unique genes of that species are combined and the characters concerned are upgraded to the highest possible level.

THE CONCEPT OF COLUMN BREEDING FOR POLYGENIC TRAITS

The column concept is based on the assumption that polygenic resistance to a certain disease in different species is based on different genes. The way of introducing a high level of stable resistance into cultivated forms according to this principle can generally be described as follows. Breed the available species with resistance to the disease separately to an acceptable level of nobilization. This results in nobilized resistant populations, each of which derives its resistance from a different species. Each population is a column of resistance, and the columns are assumed to carry different resistance genes. Therefore, intercrossing them may produce genotypes with high-level stable resistance due to the accumulation of genes from different sources. Because combination takes place after nobilization, further crosses with cultivars may at least be restricted and at best be avoided. The procedure makes sense only when different sources of resistance, or eventually other polygenic traits, are available.

An obvious application of the column concept is the use of species from the two geographically and genetically isolated gene centers of potato: South America and Central America (mainly Mexico). Based on the separate evolution of Mexican and South American species, it may be assumed that they carry different genes for agronomically important characters. Therefore, one may hypothesize that nobilized genotypes enriched with genes from Mexican species may be complementary in several respects to nobilized genotypes carrying genes from South American species. This would imply that there are good prospects for transgressive breeding based on the concept of columns.

AN INTEGRATED BREEDING PROCEDURE FOR POLYGENIC TRAITS DERIVED FROM WILD SPECIES AND PRIMITIVE FORMS

Figure 1 illustrates how the concepts of prebreeding, column breeding, and combination breeding can be integrated in one procedure. The advantages of combination breeding after prebreeding and separated nobilization are that few crosses and, eventually, no backcrosses are needed, high levels of characters may be maintained, and loss of genes is minimized.

BARRIERS TO INTERSPECIFIC HYBRIDIZATION AND WAYS TO OVERCOME THEM

Interspecific barriers in the broadest sense include all isolation mechanisms between species. When discussing barriers to interbreeding, spatial isolation, non-overlapping flowering time and cleistogamy are left out of consideration because they are real barriers only in nature, not in a breeding program.

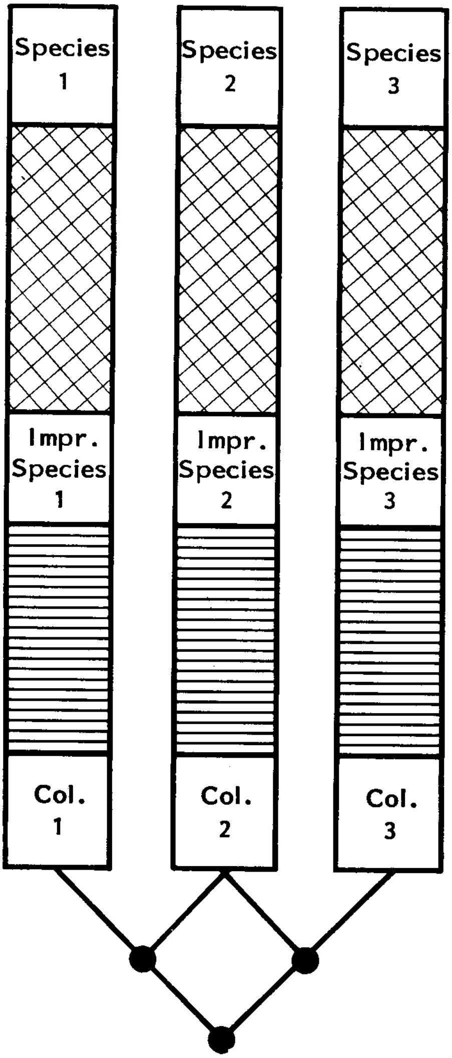
There are various kinds of barriers to interbreeding, and they may become manifest at different stages or even in different generations. Following Stebbins (1971), a distinction can be made between prezygotic and postzygotic barriers to interbreeding.

Prezygotic barriers in a breeding program are: (1) inhibition of pollen germination or pollen tube penetration of the stigma; (2) arrested pollen tube growth at different sites in style, ovary, or ovulum; and (3) single or otherwise abnormal fertilization which may lead to parthenogenesis or defective endosperm.

Postzygotic barriers are: (1) disturbance of early embryo and endosperm development due to somatoplastic sterility, elimination of chromosomes, and other expressions of disharmony; (2) failure of shrivelled or even normal seeds to germinate; (3) (sub)lethality and other abnormalities during F_1 plant growth; (4) male sterility or poor flowering of F_1 plants; and (5) disharmonious genotypes in segregating generations causing hybrid breakdown.

Prezygotic barriers have been overcome or circumvented more or less successfully in different ways. Using large numbers of female plants and a pollen mixture from many males may be advocated in view of genotypic differences in crossability. Cutting of styles and direct pollination of ovules has been reviewed by Rangaswamy (1977).

The results of using "mentor pollen" are different. Stettler (1968) was successful with *Populus* as were Willing and Prior (1976), who got good results from treatment of stigmas with chemicals. Use of immunosuppressants (Bates, 1975) in cereals has given little success.



Preferably diploid species as sources of genes.

Prebreeding within each species using different accessions per species: evaluation + inheritance studies + concentration of polygenes + combination of different characters.

Improved species: upgraded levels of polygenic traits and different characters combined.

Nobilization via crosses and backcrosses with cultivated material:
—separately per species
—preferably at diploid level.

Nobilized "columns."

Combination breeding at nobilized level.

Figure 1. An integrated breeding procedure for polygenic traits from wild species and primitive forms. Impr. = improved; Col. = column.

Embryo culture is an indispensable procedure when the endosperm is defective (Raghavan, 1977; and Jensen, 1976). The embryos should be sufficiently large. F_1 sterility may be overcome by chromosome doubling if it is caused by lack of homologous pairing. This is not the case when sterility is due to sterility genes, cytoplasmic-genic interactions, or disharmonious gene combinations, but then sterility is often restricted to male gametes. However, female fertility may also be low in hybrids and may cause difficulties when backcrossing is needed (Lapchenko, 1962).

Environmental factors are important in interspecific hybridization, because unstable genotypes are more sensitive to unfavorable conditions than stable ones. When crosses between wild species and cultivars do not succeed at all, the breeder has to resort to so-called bridging species, which are crossable with both cultivar and wild species. Problems related to this procedure have been discussed earlier. A few examples of the use of double bridges will be given below.

Reciprocal differences are very common in interspecific hybridization. In most cases it is not predictable which will be most successful. Therefore, it is advisable to make routinely interspecific crosses reciprocally. An important exception is the rather general phenomenon that when self-incompatible and self-compatible species are intercrossed, a cross between a self-compatible female x self-incompatible male is most successful. This "unilateral incompatibility," first described by Lewis and Crowe (1958), has been observed in nearly all plant families which comprise both self-compatible and incompatible species (Abdalla and Hersen, 1972; and de Nattancourt, 1977).

EVOLUTIONARY ASPECTS OF INTERSPECIFIC BARRIERS

Gene exchange between species in nature is restricted or completely absent. Without interspecific barriers, species would become submerged in one gene pool. Ecological or geographic isolation of subpopulations of a species may initiate the evolution of new species due to natural selection in different environments. An isolated population may become genetically divergent from the original species to such an extent that upon artificial intercrossing with the original species, postzygotic barriers become manifest. Prezygotic barriers may evolve between sympatric forms due to natural selection against fertilization by alien pollen. They may also evolve in the presence of previously developed postzygotic barriers. A detailed description of these processes is presented by Stebbins (1971, chapter 5).

GENETIC ASPECTS OF INTERSPECIFIC BARRIERS: A GENETIC MODEL

A cross between two species is successful if there is a normal relationship between pollen and pistil parent. A normal relationship implies that, after pollination, a chain of processes can take place unhampered. This requires perfect coordination and interaction between gene (complexes) in the pollen (parent) and matching gene (complexes) in the pistil parent. According to Hogenboom (1975), each of the matching parental genes or gene complexes controls a link in the chain of processes and interactions which are needed for successful hybridization. Incomplete matching may cause one or more missing links in the chain and may thus inhibit interbreeding. In this case, there is a lack of genetic information in one species about some character in the other. For this phenomenon, Hogenboom (1973) introduced the term "incongruity," which is genetically different from incompatibility based on oppositional action of equal S-alleles in pollen (or pollen plant) and pistil. In relation to incongruity as far as it is expressed between pollination and fertilization, Hogenboom proposed the terms "penetration capacity" and "barrier capacity." Penetration capacity is determined by all genes or gene complexes in the pollen which control its capacity to overcome or circumvent barriers against hybridizing alien females. Barrier capacity comprises the genes or gene complexes controlling all barriers on the female side against being hybridized by alien pollen.

INTERSPECIFIC CROSSABILITY

Crossability between species is determined by the genotypes of both parental species according to Hogenboom's model for incongruity. Hermsen et al. (1977) reported results from interspecific *Solanum* crosses that suggested a gene-for-gene relationship between male and female parent; the crossability spectrum found resembled reaction spectra displayed by many host-parasite systems. There are several reports on genetic determination of crossability between species (Lein, 1943a, 1943b; Grun and Aubertin, 1966; Pickering and Haynes, 1976; Hermsen, 1966; Hermsen et al., 1974; and Hogenboom, 1972). In outbreeding species, only certain genotypes of one species may be crossable with certain genotypes of the other. If these crossability genotypes are scant in either species, the probability of getting a combination that fits is small. A statement that two species are not crossable is controversial unless a broad genetic variation of the parental species has been used and the cross combinations have been carried out on a large scale under a wide range of environmental conditions (Hermsen, 1979).

SOME EXPERIMENTAL RESULTS

Figure 2 shows the production of tetra- and hexaploid double-bridge hybrids in *Solanum*. Only *S. bulbocastanum* has the high level of late blight resistance that could be transferred through two susceptible bridging species into part of the hybrids with *S. tuberosum*. *S. bulbocastanum* and *S. tuberosum* are fully isolated species. *S. acaule* is crossable only as female with *S.*

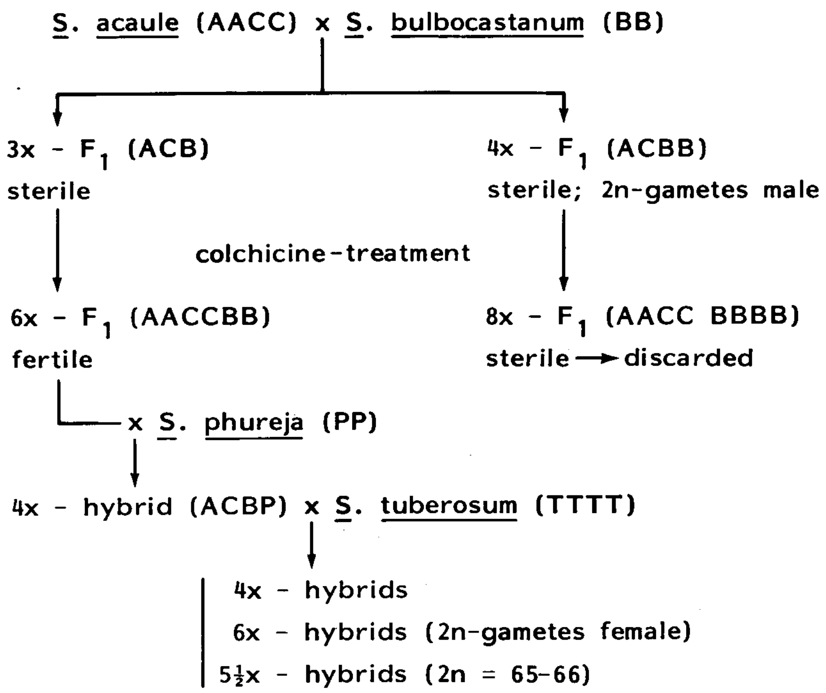


Figure 2. Double-bridge hybrids between *Solanum bulbocastanum* and *S. tuberosum*. In parentheses: indication of genome composition. Ploidy levels: 3x, 4x, 6x; x = 12.

Table 1. Crosses made by Matzk et al. (1980) between three species each of *Festuca* and *Lolium* as females and four to nine predominantly apomictic polyploid species of *Poa* as males.

Female parent (ploidy)	No. of *Poa* species (male)	No. of ♀ plants avg.	No. of ♀ plants range	Total no. of florets pollinated
Festuca pratensis (2x, 4x)	9	7.6	1-41	17,686
Fustuca arundinacea (6x)	9	4.3	1-20	12,392
Festuca gigantea (6x)	4	2.5	1-5	5,512
Lolium perenne (2x, 4x)	9	4.2	1-24	9,357
Lolium multiflorum (2x, 4x)	9	9.9	2-38	16,819
Lolium hybridum (2x, 4x)	5	5.8	1-18	5,702

bulbocastanum. Both the triploid and the tetraploid hybrids (2n gametes from *S. bulbocastanum*) were completely sterile. Doubling through colchicine resulted in fertile hexaploids, but the octaploids were still sterile and had to be discarded. Crosses between the hexaploids and diploid *S. phureja* besides some trihaploids also produced a large amount of shrivelled seeds, of which the major part germinated normally, giving rise to the tetraploid hybrid with the genome composition ACBP (chromosome number ranging from 42-48). About 160 of these plants (18,000 flowers) were pollinated with cultivars and 25 of them produced nearly 200 seeds in total, giving a total of 40 hybrids. So there were strong barriers between the ACBP-tetraploid and the cultivars, which could be overcome owing to the large-scale pollinations. The final hybrids segregated for late blight resistance. Most of them intercrossed freely and displayed only weak barriers to further crosses with varieties (Hermsen and Ramanna, 1973).

Comparable results were obtained in attempts to intercross a wild non-tuberbearing *Solanum* species with tuberbearing wild species (Hermsen and Taylor, 1979). Also, in this case, two wild bridging species enabled a final hybridization with cultivars.

Extensive investigations on interspecific and intergeneric crosses were carried out by Matzk et al. (1980) in grasses. On twelve plants of tall fescue (*Festuca elatior*) used as female parent, 1,800 florets were pollinated with cocksfoot (*Dactylis glomerata*); only from one plant were three hybrids obtained. In this plant, pollen tube growth was nearly normal, whereas in the other eleven plants, pollen tube growth was inhibited. Another large-scale crossing program was carried out (Table 1) involving three species each of *Festuca* and *Lolium* (♀) with nine mainly apomictic polyploid *Poa* species.

Table 2. Crosses made by Matzk et al. (1980) from 1976-1978 of *Festuca* and *Lolium* species with the following tropical grasses: 1. *Agropyron scabrum*, 2. *Cenchrus ciliaris*, 3. *Panicum maximum*, 4. *Paspalum dilatatum*, 5. *Pennisetum purpureum*, 6. *Eragrostis curvula*.

Female parent (ploidy)	Male parents (nos. refer to caption)	No. of ♀ plants avg.	No. of ♀ plants range	Total no. of pollinated florets
Festuca pratensis (2x, 4x)	1,2,3,4,5,6	4.6	1-8	4,421
Festuca arundinacea (6x)	1,2,3,5	5.3	3-7	4,470
Festuca gigantea (6x)	3	2.0	2	402
Lolium perenne (2x, 4x)	2,3,4,5,6	3.6	1-6	3,674
Lolium multiflorum (2x, 4x)	1,2,3,4,5,6	9.5	3-26	9,689
Lolium hybridum (2x, 4x)	2,3,4,5	4.5	3-7	3,515

The three species are sympatric. In spite of application of mentor pollen, growth substances, irradiation, cutting styles, and extension of crossing over four successive years, not one hybrid plant was obtained from 67,468 pollinated florets. Pollen germinated badly, and pollen tubes spiralized, thickened, or burst in the styles. Only in cross combinations where several thousands of florets of many female plants were pollinated did a few embryos start to grow, but they aborted prematurely.

A third large program was comprised of crosses between the same *Festuca* and *Lolium* species as females with six apomictic tropical grasses (Table 2) as males. *Festuca* and *Lolium* species and the tropical species are allopatric and have evolved in highly different environments. *Lolium* and *Festuca* have a C_3-assimilation pathway and $x = 7$; the tropical grasses have a C_4-assimilation pathway, and x is mainly 9. In view of the separate evolution, strong postzygotic barriers were expected and indeed found. Prezygotic barriers were hardly expected because of their allopatry. However, normal pollen growth was observed only in the crosses with *Cenchrus* and *Pennisetum*. In no case were hybrid plants obtained in spite of embryo culture and size of the program.

DISCUSSION

Evaluation is one of the key words for a manager of a gene bank. When accessions are being evaluated, notes are taken of the results, stored in a computer and eventually published. Most so-called resistant accessions, when inoculated, segregate for resistance. Accessions could be improved during the evaluation procedure by intercrossing resistant plants or collecting open-pollinated fruits from such plants. In this way, new accessions with higher frequencies of resistance genes are bred. Genetic drift could be avoided by growing a somewhat larger number of plants per accession. Stepwise upgrading accessions of wild species for one or more characters would contribute greatly to their usefulness in breeding. Breeding columns for polygenic traits as well as prebreeding may be too laborious to be applied for several such traits and in several species. The concepts as such are correct and should be kept in mind when utilizing wild species. In practice, however, the breeder will try and grasp as many useful characters out of a species as possible, because the nobilization process may be time consuming.

Experiments are presented to illustrate severe breeding barriers. They are not representative for most interspecific crosses. Many species are closely related to the crops to be improved and sometimes the hybrids can be handled like intervarietal crosses. The availability of closely related species varies greatly between crops. Only when remote species carry exceptionally valuable genes not found in closer-related species, such large-scale programs may be rewarding.

Somatic hybridization sometimes is advocated in cases of remote hybridization. If successful, it has some advantages. Sterile or poorly flowering plants can be hybridized, as well as very young plants. Furthermore, heterozygous valuable genotypes are not disrupted, and the hybrids obtained may be immediate allopolyploids if no chromosome elimination occurs. On the other hand, only one hybrid genotype is obtained from two parental genotypes. Backcrosses, which may be more difficult that the original cross, cannot be made through a second cycle of somatic hybridization, because the chromosome number will reach levels too high for normal functioning. Somatic hybrids from very remotely related parents may suffer from inviability, sterility, and instability, but even if they are fertile, preferential pairing may prevent the necessary gene recombinations. There is a real risk of a dead end.

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