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NATURE, EVOLUTION, AND BREEDING OF POLYPLOIDS

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ABSTRACT. Different kinds of polyploids are defined and characterized by their genome formulas. It is emphasized that natural polyploids range in genome composition from true autopolyploids to true allopolyploids. The origin and evolution of polyploids is discussed, and special attention is paid to the role of numerically unreduced or 2n gametes.

Methods of inducing autopolyploidy are mentioned along with the requirements that diploid crops should meet in order to obtain useful results from somatic doubling. Methods of resynthesizing existing allopolyploid crops or synthesizing new ones are evaluated and the main requirements for success discussed. It is emphasized that genetically broad initial material is indispensable both for induction of autopolyploids and for (re)synthesis of allopolyploids that are to be useful for breeding.

Some characteristic features relevant to the breeding of autopolyploids are described with emphasis on the effects of di-allelism and multi-allelism on inbreeding depression and heterosis. Also some particular characteristics of allopolyploids are treated, and some unconventional breeding approaches are briefly discussed.

Index Descriptors: polyploidy, evolution, breeding, somatic doubling, 2n gametes, multi-allelism, heterosis, and inbreeding depression.

INTRODUCTION

Polyploids are plants combining three or more basic genomes. Plants have a characteristic genome composition that can be described conveniently by genome formulas. The most general formula is:

$$2n = p_A x_A + p_B x_B + \ldots\ldots$$

where 2n = the somatic number of chromosomes,

$x_A, x_B \ldots$ = the basic genomes of ancestral species A, B, . . ., and

$p_A, p_B \ldots$ = the frequency of each basic genome.

Kihara and Ono (1926) introduced the terms auto- and allopolyploids. They state that doubling of the same chromosome set leads to autoploids, whereas allopolyploidy is the result of interspecific hybridization followed by chromosome doubling. As will be explained below, these definitions are too simple a description of what really occurs in nature and in plant breeding.

True autopolyploids trace back to one diploid species or to different species or ecotypes carrying homologous chromosomes. Their general genome

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formula is simply $2n = px$, there being only one type of basic genome consisting of x different chromosomes, and each chromosome at a frequency of p, the ploidy level (p is a whole number $\geqslant 3$). As the chromosomes each are represented by three or more homologous copies, each gene is represented by three or more alleles. These alleles may be equal (homozygosity or mono-allelism) or different (heterozygosity: di-allelic, tri-allelic, ... , multi-allelic). Some examples of natural autopolyploids with their genome formulas are banana (*Musa sapientum*) cv. Gros Michel ($2n = 3x = 33$), orchardgrass (*Dactylis glomerata*) ($2n = 4x = 28$), alfalfa (*Medicago sativa*) ($2n = 4x = 32$), potato (*Solanum tuberosum*) ($2n = 4x = 48$), timothy grass (*Phleum pratense*) ($2n = 6x = 42$), and crested wheatgrass (*Agropyron cristatum*) ($2n = 4x$ or $6x = 28$ or 42). Artificial autopolyploids have been bred successfully from diploid clovers, grasses, beets, and ornamentals.

True allopolyploids trace back to two or more related diploid species, the chromosomes of one species being non-homologous or homoeologous with the chromosomes of the other progenitor species. Each ancestral genome is represented twice in allopolyploids. So the general genome formula of allopolyploids is $2n = 2x_A + 2x_B + \ldots$ (c.f., diploids $2n = 2x$). Only homologous chromosomes pair at meiosis, forming bivalents, whereas homoeologous chromosomes from different ancestors do not pair owing either to lack of homology or to the action of genes preventing "homoeologous" pairing. Therefore, allopolyploids are functional diploids, but the inheritance of most characters may be more complicated than in diploids depending on the degree of the relationship between the ancestral species. Allopolyploids are rather frequent among wild species. Several important crops are allopolyploids, e.g., wheat (*Triticum aestivum*), oats (*Avena sativa*), and tall fescue (*Festuca elatior*) ($2n = 2x_A + 2x_B + 2x_C = 42$), tobacco (*Nicotiana tabacum*) ($2n = 2x_S + 2x_T$), cotton (*Gossypium hirsutum*) ($2n = 2x_A + 2x_D = 52$) and rape-seed (*Brassica campestris*) ($2n = 2x_A + 2x_C = 38$). Mention should be made of some potential new crops, synthesized from existing ones: Triticale (wheat and rye), Festulolium (fescue and ryegrass), Raphanobrassica and Brassicoraphanus (from subspecies of *Raphanus sativus* and either *Brassica oleracea* or *Brassica campestris*).

It should be emphasized that most natural polyploids are not truly auto- or alloploid but range in genome constitution from true autoploids to true alloploids. This situation has been described by the term segment-allopolyploidy (Stebbins, 1950), which may occur to different degrees in part of or even in all chromosomes of a polyploid. In terms of chromosome pairing, this means that in alloploids, apart from preferential pairing between homologous chromosomes, also some degree of homoeologous pairing may occur. Furthermore, in autoploids pairing between homologous chromosomes may not be fully random but slightly preferential, indicating some degree of homoeology. In terms of the genetics of qualitative characters, this situation implies the occurrence of disomic, tetrasomic, and intermediate ratios for different characters in progenies from the same plant. Similarly, it is conceivable that genes controlling a polygenic trait follow different inheritance patterns such that neither disomic nor tetrasomic quantitative genetic models fit the real situtation, apart from other deviations from reality that are inherent in such models.

ORIGIN AND EVOLUTION OF POLYPLOIDS

Polyploidy is common in many genera, and many species comprise diploid as well as polyploid plant types. Polyploidy was long believed to originate in nature mainly from spontaneous somatic doubling of the chromosome number in zygotes or meristems in response to stress conditions. One well documented case (Newton and Pellew, 1929) of natural somatic doubling is the origin of *Primula kewensis*. However, spontaneous somatic doubling in nature will rarely produce plants that can survive competition with their diploid counterparts owing to decreased fitness. On the other hand, polyploidy through the production and sexual functioning of restitution (or 2n) gametes is the most common and widespread mode of natural polyploidization. It may occur in every species or ecotype after selfing and after intraspecific, interspecific, and intergeneric hybridization. Its importance in the origin and evolution of polyploids has been amply discussed by Harlan and de Wet (1975), Skiebe (1975), and Den Nijs and Peloquin (1977a, 1977b). Harlan and de Wet (1975) think of the origin as a two-step process: (1) $\underline{\mathrm{AA}}$ x BB → AAB and (2) $\underline{\mathrm{AAB}}$ x BB → AABB, the underlined parent producing the 2n gametes. The origin of polyploids from diploids is more complicated than would appear from Harlan and de Wet (1975) even when typical interspecific and intergeneric barriers are left out of consideration. The factors that may affect seed set and the resulting ploidy levels in the offspring are of special interest to plant breeders and will be discussed in the paper on sexual polyploidization along with different mechanisms of 2n gamete formation and their potentials for breeding polyploid crops.

Equally important as the frequency of their origin is the chance of survival or the competitive ability of new polyploid embyros and plants. Here again 2n gametes and their mode of origin enter the picture. In nature few polyploids survive beyond one generation. They must compete for the habitat of their diploid parents or colonize new habitats. Most newly produced polyploids, both auto- and alloploids, are less fertile than their diploid parents. However, 2n gametes are continuously produced and thus bring about a continuous production of new polyploids. Furthermore, if 2n gametes are involved that have originated from first division restitution (FDR, explanation later), the new polyploids may be even more vigorous than diploids. Perennial polyploids have a competitive advantage over annuals, because they have several generations to produce new gene combinations with increased fitness. Many annual polyploids, however, have been equally successful. Spontaneous hybridization with the diploid parents or related species occurs in nature and increases the variability of the polyploids. In this hybridization process, 2n gametes may contribute in different ways to the success of polyploids: 2n eggs of triploids (2n = 3x) may fuse with reduced sperm cells of diploids or reduced egg cells of tetraploids may fuse with 2n gametes of diploids, both processes giving rise to new tetraploids. These tetraploids, if FDR-2n gametes are involved, may be highly vigorous, adaptive and fertile (Den Nijs and Peloquin, 1977b).

ARTIFICIAL INDUCTION OF AUTO- AND ALLOPOLYPLOIDY

Breeders used to apply colchicine and presently also use in vitro explant culture (Jacobsen, 1977) for inducing somatic doubling of chromosome numbers. Somatic doubling may be induced for several reasons:

1. To obtain artificial autopolyploids from diploid crops;
2. To resynthesize existing allopolyploid crops from their diploid ancestral species and to synthesize new allopolyploid crops from existing crops;
3. To produce allopolyploids for use as fertile bridges for gene transfer into varieties;
4. To improve crossability between parents with different ploidy levels by equalizing their functional ploidy.

The subjects 1 and 2 will be discussed in this paper; 3 and 4 will be discussed in my paper on the use of wild species in this issue, pp. 461-474.

Artificial induction of autotetraploidy in diploid crops

The prerequisites for successful somatic doubling of diploid crops were first proposed by Levan (1945). They are: (a) a sub-optimal number of small chromosomes, (b) outbreeding as the chief mating system, and (c) cultivation primarily for vegetative parts or flowers. Also perennial growth habit and vegetative reproduction may contribute to the success of somatic doubling of diploids. These conditions are logical, because somatic doubling leads to larger plant cells and organs and reduces fertility. As a matter of course, a genetically broad starting material is a basic requirement for success, because breeding mostly begins after doubling.

It is interesting to note that the natural autopolyploids predominantly meet the requirements mentioned by Levan (1945). The same holds true for the rather successful artificial autopolyploids, which still are few in number, e.g., some grasses and clovers, beet, watermelon, and ornamentals. On the other hand, extensive long-term experiments with doubled diploid seed crops like barley (*Hordeum vulgare*), maize (*Zea mays*), sorghum (*Sorghum bicolor*), and rye (*Secale cereale*) have hardly been successful. This holds true also for the efforts to improve sufficiently the fertility of artificial autotetraploids by mutagenic treatments aimed at inducing some degree of preferential pairing or allopolyploidization (Gaul and Friedt, 1975; Doyle, 1979; and Sybenga, 1973).

More promising than somatic doubling is the search for diploid plants producing 2n FDR-gametes either male, female, or both. Such diploids can be used in crosses with already available autotetraploids (unilateral sexual polyploidization) or in diploid x diploid matings (bilateral sexual polyploidization). This approach is near to practical application in potato and alfalfa and will be discussed in a separate paper in this issue, pp. 435-448.

(Re)synthesis of allopolyploids

Nature has been successful in synthesizing allopolyploids for a large number of crops and numerous wild species that are allopolyploids. MacKey (1970) demonstrated that most natural allopolyploids have originated by incorporation of genomes from autogamous and allogamous ancestral species into an amphiploid. In the resulting alloploids, autogamy is generally retained. Breeders have not been very successful in producing important crop plants through induced allopolyploidy. It may seriously be questioned whether the main requirements for successful (re)synthesis have always been taken into account:

First, the right forms of the parental species have to be chosen in terms of crossability, degree of relationship and breeding aims.

Second, the genetic variation in the initial material should be adequate for preselecting superior genotypes carrying genes for desirable simply inherited characters and sufficient variability for polygenic traits. This is a must for newly synthesized crops like Triticale, and it is desirable for resynthesized crops like *Brassica napus*, because raw allopolyploids have to be improved further to reach the varietal level.

Third, (re)synthesis should be carried out on a large scale using the right method of synthesis in order to obtain sufficient variation among the raw allopolyploids. Basically there are two different methods: (1) intercross the diploid parental species and double the F_1 hybrids, and (2) double the diploid parental species and intercross the autotetraploids. In choosing method 1 or 2 the following factors are relevant. Crossability between parental species is often more difficult at the autotetraploid level due to decreased fertility. A second factor is that doubling as a rule is only partly successful and plants may be lost during the doubling procedure. This is no problem with method 2, where many seeds of the parents are available, but it may be troublesome with method 1 because the amount of F_1 seeds usually is limited. A third aspect is meiotic instability in the autopolyploids with method 2, which may lead to more aneuploid allopolyploids than with method 1. The most important implication is a genetic one: method 1 invariably leads to completely homozygous allopolyploids, whereas with method 2, an appreciable amount of heterozygosity of the parental species is still present in the raw allopolyploids. This means a greater potential for further improvement.

When species are available with the ability to produce 2n FDR-gametes, it is to be preferred to make use of this character like nature does. A promising approach would be to cross doubled superior plants of an autogamous species with superior FDR-diploids of an allogamous species followed by further breeding.

ASPECTS OF BREEDING AUTOPOLYPLOID CROPS

All known autopolyploid crops are outbreeders. They are rather intolerant of homozygosity and consequently need much heterozygosity for maximum performance. Another common feature is polysomic inheritance with the potential of random chromatid assortment in different degrees, the coefficient α varying from 0 to 1/7. Therefore, large populations are needed for selection and breeding. Producing homozygous lines by conventional means is not at all feasible.

Breeding of autopolyploids is also hampered by the widespread occurrence of aneuploidy, mainly in recent polyploids. This may strongly affect not only seed fertility but also the yield of vegetative parts (Simon, 1966). Selection for euploidy does not eliminate aneuploidy. Normally a balanced percentage of aneuploids develops, which may shift along with changes in the environment (Maizonnier and Picard, 1970).

Owing to their polysomy, autopolyploids have the potential to develop optimal dosages of favorable alleles (nulliplex, simplex, duplex, triplex, quadruplex) and to evolve multiple allelic series for many loci. Thus, during their evolution natural old autopolyploids have achieved a precise genetic balance for quantitative and qualitative characters in terms of allelic interaction and of dosage relationships and have developed mechanisms to exploit types of heterotic interactions not possible in disomic inheritance (MacKey, 1970; Bingham, 1980).

On the other hand, the overall average number of alleles per locus is restricted in recently developed autopolyploids. The frequency of diallelic duplex, simplex, and triplex loci then is relatively large. This may lead to phenotypically stable, uniform autopolyploid populations. This characteristic has been exploited in breeding autotetraploid freesia and other flower crops from diploids. When compared to their diploid counterparts, autotetraploid populations are uniform to such an extent that seed propagation may replace the conventional clonal propagation (Sparnaaij, 1979).

In diploids and allopolyploids and in raw autotetraploids that are obtained directly from heterozygous diploids through somatic doubling, the maximum number of alleles per locus is two. This implies only one type of heterozygous allelic interaction. In autotetraploids tetra-allelism (= four alleles per locus) represents the maximum level of heterozygosity at a locus. This implies eleven possible hetero-allelic interactions, six of them being interactions between pairs of alleles (so-called first-order interactions).

Extensive theoretical and experimental research on heterosis and inbreeding depression in natural as well as in induced autopolyploids has been carried out, especially since the early 1960s (Demarly, 1963; Dudley, 1964; Busbice and Wilsie, 1966; Lundqvist, 1966; Berninger, 1967; Gallais, 1967a, 1967b; Dewey, 1966, 1969; Dunbier and Bingham, 1975; and Mendoza and Haynes, 1973, 1974). It has been well established that upon inbreeding, heterozygosity decreases much slower in autopolyploids than in functional diploids, the rate of decrease being $(5 - 2 \alpha)/6$ and $1/2$, respectively, per generation of selfing. Consequently, inbreeding depression should be less in autopolyploids than in functional diploids. It has been demonstrated that in artificial autopolyploids with mainly diallelic heterozygous loci, inbreeding depression is indeed directly related to the standard coefficient of inbreeding (Lundquist, 1966; and Rice and Dudley, 1974). However, in natural autopolyploids, it was found to be significantly larger and similar to the expected rate at which first-order interactions were lost from tri- and tetra-allelic loci (Busbice and Wilsie, 1966; Dewey, 1966, 1969; and Mendoza and Haynes, 1973, 1974). It was apparent from these investigations that multiple allelic interactions are predominant in natural autopolyploids.

This conclusion is corroborated by the results of experiments on heterosis in lucerne, crested wheatgrass, and potato on the one hand and induced autotetraploid rye and maize on the other by the aforementioned authors. They found the ranking in performance to be correlated with the increase in frequency of tetra-allelic loci. This suggests that heterosis is maximized by maximum heterozygosity. Dunbier and Bingham (1975) and Bingham (1980), in his excellent review on this topic, demonstrated with alfalfa that not only the diversity of parental genotypes but also the mating system of the selected parents (single cross, double cross, synthetic variety at equilibrium) to develop varieties are of prime importance for successful breeding of autopolyploid crops. The authors concluded that double cross varieties capitalize on potential maximum heterozygosity, but synthetic varieties usually do not because the peak frequency of tri- and tetra-allelic loci has passed when equilibrium is approached. However, the production of double cross seed in seed-propagated autotetraploid fodder crops is not yet economically feasible.

A potentially powerful method to maximize heterozygosity and to keep sufficient uniformity would be the use of diploids that produce 2n gametes through FDR. The method is particularly useful in the asexually reproduced potato. In alfalfa, it might become feasible, once diploid genotypes are available that combine excellent agronomic characteristics with a stable high-frequency production of FDR-gametes, thus enabling an efficient production of high-standard F_1 seed from tetraploid x diploid crosses.

ASPECTS OF BREEDING ALLOPOLYPLOID CROPS

Allopolyploids are predominantly autogamous, basically homozygous, and functionally diploid. They differ from true diploids in having two or more divergent but related genomes. So they may have a built-in hybridity among loci with similar function in the genomes. With their disomic inheritance and fixed "heterozygosity," they have the potential of benefitting from both self- and cross-fertilization systems.

Preferential pairing of homologous chromosomes (bivalents) is most characteristic of true allopolyploids. Homoeologous chromosomes do not pair as a consequence of either structural differentiation or the functioning of pairing regulating genes. Pairing regulation has been most profoundly investigated in wheat (Review: Sears, 1976).

As mentioned before, there is homozygosity in the genome set from each ancestral species, but similar loci from different ancestral species may be "heterozygous." This fixed heterozygosity may result in fixed heterosis. However, various other interactions are known to occur, for example, complementary interaction, mutual weakening, and cumulative polymerism. These phenomena cause the so-called "damping effect" of allopolyploidy. This may complicate genetic research, obscure phenotypic classes, and thus hamper the selection of desirable genotypes.

Apart from conventional breeding of allopolyploids, a number of unconventional approaches are being investigated. The idea of crop improvement through manipulating separate chromosomes by means of chromosome substitutions in existing varieties dates back to the 1950s. E. R. Sears was the first to produce series of auto-substitution lines with *Triticum aestivum* L. "Chinese Spring" as receptor. Unrau (1958), using Sears' material, proposed methods for their application in breeding.

Chromosome engineering received a new impetus in the 1960s by the work of Law and associates (1966), who also organized international cooperation in the European Wheat Aneuploid Cooperative. This cooperation was aimed at producing sets of reciprocal substitution lines of some leading varieties from all over Europe in order to evaluate separate chromosomes for their contribution to qualitative and quantitative characters and to improve varieties by chromosome engineering.

Another approach, isolation and improvement of component genomes of allopolyploids followed by resynthesis, was initiated with wheat by Kerber (1964) and continued by Siddiqui (1972). Although this laborious approach has never reached practical application in wheat breeding, it has clearly demonstrated the tremendous change of component genomes during the evolution after having been incorporated into an allopolyploid. Earlier genetic research in cotton and tobacco by Gerstel and Phillips (1958) had already shown clear differences between the genomes in these allotetraploids and the corresponding genomes of their diploid ancestors.

The two approaches have been mentioned here in order to explain the imbalance in raw allopolyploids, the genomes of which have not yet been fully adapted in the same individual. Raw allopolyploids can only serve as initial material for breeding new crops and as intruments to improve existing allopolyploid crops by a general broadening of the genetic base of breeding or to transfer desirable genes from wild species into cultivars.

Among the non-conventional approaches to breeding allopolyploid crops, the doubled-haploid (DH) technique should be mentioned. This will be further explained and evaluated in the concurrent papers on haploidy. Suffice it to state that the results obtained so far justify the conclusion that this technique is promising for future breeding of diploids as well as of allopolyploids.

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