

CHAPTER TWENTY-THREE

Types of Polyploids

Development of a Classification

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The distinction between autopolyploids and allopolyploids (or amphiploids) is fundamental. It is also a qualitative distinction which oversimplifies the actual situation. Kihara and Ono (1926) originally expressed the distinction in broad terms. Autopolyploidy, in contradistinction to allopolyploidy, is the doubling of one and the same chromosome set.

In the first edition of *Recent Advances in Cytology*, Darlington (1932) restated the distinction as follows. An autopolyploid is a polyploid derived by doubling or adding the chromosome sets of a structural homozygote; hence it is an organism containing three or more sets of homologous chromosomes. By contrast, an allopolyploid is the product of doubling in a species hybrid; it is therefore a polyploid containing separate sets of nonhomologous chromosomes (Darlington 1932:169).

It was clear to the early students of the subject that a complete intergradation exists between homologous and nonhomologous chromosomes, between structural homozygotes and structural heterozygotes, and between homozygous individuals and interspecific hybrids. Autopolyploidy and allopolyploidy as defined above are thus the extreme members of a graded series. Further subdivision of these opposite classes to recognize various intermediate conditions may be convenient for many purposes.

Müntzing (1936a:310 ff.), after discussing various definitions of autopolyploidy, arrived at the following concept. Autopolyploids have multiple chromosome sets which are identical structurally, but which may be different genically. Clausen, Keck, and Hiesey (1945:70 ff.) then went on to distinguish two main types of autopolyploids: those arising from fertile interracial hybrids and those arising from ordinary nonhybrid individuals.

Darlington (1932) recognized three nodal conditions of allotetraploidy on the basis of the degree of structural differentiation between the constituent genomes. The three conditions are exemplified by *Raphanobrassica*, *Primula kewensis*, and *Crepis rubra-foetida*. The main facts concerning *Raphanobrassica* and *P. kewensis* were presented earlier, in chapter 19, to which the reader is referred for the details.

In the extreme case, as found in *Raphanobrassica*, the genomes are strongly differentiated structurally, so that the chromosomes do not pair in the diploid hybrid, but do form bivalents regularly in the tetraploid derivative. The intermediate condition, represented by *Primula kewensis*, is that where the chromosomes are somewhat less strongly differentiated structurally, so that they regularly pair in bivalents in both the diploid hybrid and the tetraploid derivative. Slight structural differentiation of the parental genomes, as between *Crepis rubra* and *C. foetida*, permits bivalent pairing in the diploid hybrid and extensive quadrivalent formation in the tetraploid derived from it. This third type of allopolyploid thus approaches an autopolyploid in its cytogenetic behavior (Darlington 1932:170).

Later authors have elaborated on this general theme. Clausen, Keck, and Hiesey (1945:70 ff.) classify amphiploids on two interrelated features, namely, the strength of the sterility barrier between the parental species, and the degree of chromosome pairing between the parental genomes. *Raphanobrassica* in their system is an intercenospecific amphiploid with nonpairing genomes; *Primula kewensis* is an interecospecific amphiploid with intergenomic pairing; and there are various intermediate combinations. Stebbins introduced the useful terms segmental allopolyploid and genomic allopolyploid to designate the *P. kewensis* type and the *Raphanobrassica* type of amphiploid respectively (Stebbins 1947a, 1950:315).

At the hexaploid, octoploid, or higher levels, it is possible for a plant to be simultaneously both an autopolyploid and an allopolyploid. This

type of polyploid is aptly called an autoallopolyploid. It arises from a hybrid between two specifically and genomically distinct parents, one or both of which is an autopolyploid. Thus hybridization between an autotetraploid and a genomically different diploid will yield a triploid hybrid, which on doubling produces a hexaploid containing four sets of one genome and two sets of the other.

Let us summarize this discussion by listing the principal types of polyploids together with their genomic constitutions. Following the standard convention, a given genome is represented by a letter of the alphabet. Genomes *A*, *B*, etc., are strongly differentiated structurally so that their chromosomes usually fail to pair in the interspecific hybrids. Genomes or subgenomes *A_s*, *A_t*, etc., are differentiated structurally to an intermediate degree, so that partial or complete bivalent formation takes place in both the diploid hybrid and the amphiploid derivative. The diploid species which produce, singly or in combination, the various kinds of polyploids are *AA*, *A_tA_t*, *BB*, etc.

I. Autopolyploids

1. Strict autopolyploid. *AAAA*
2. Interracial autopolyploid. *AAAA*

II. Amphiploids

3. Segmental allopolyploid. *A_sA_sA_tA_t*
4. Genomic allopolyploid. *AABB*
5. Autoallopolyploid. *AAAABB*.

It will be noted that types 2, 3, 4, and 5 are hybrid polyploids, whereas only type 1 is non-hybrid.

Cytological Criteria

The principal criteria for distinguishing between autopolyploids and amphiploids are chromosome behavior, fertility, segregation ratios, and morphology. These criteria all break down in individual cases. Known amphiploids frequently exhibit the cytogenetic behavior of autopolyploids, and vice versa.

The most obvious aspect of chromosome behavior which is expected to differ as between autopolyploids and amphiploids is the presence or absence of multivalents at meiosis.

Multivalent formation, however, is limited by chiasma frequency, which in turn is affected by chromosome size and genetic conditions. Because of these limiting factors, autotetraploids nearly always have less than the maximum possible number of quadrivalents. Thus autotetraploid rye (*Secale cereale*, $x = 7$) shows a range of 0 to 6 quadrivalents per cell, where 7 IV would represent maximum pairing, and the average quadrivalent frequency varies between 2 and 4 IV in different strains (Müntzing and Prakken 1941; Jain 1960).

On the other hand, a segmental allopolyploid may and often does exhibit some multivalent formation. Tetraploid *Primula kewensis*, for example, usually forms bivalents, as we have seen earlier, but does have occasional quadrivalents. The occurrence of multivalents in this and other segmental allopolyploids is to be expected from the partial homology between chromosomes belonging to the different subgenomes.

If these homeologous chromosomes can pair in the diploid hybrid, they can also pair occasionally in the amphiploid derivative. Preferential pairing, in other words, may not be completely effective. This intergenomic (or so-called heterogenetic) pairing may simply produce bivalents. But, if the heterogenetic pairing is combined with normal homogenetic pairing in the same pairing partners, higher associations such as trivalents and quadrivalents will be formed. In a segmental allotetraploid of the genomic constitution *A_sA_sA_tA_t*, the four chromosomes belonging to any given chromosome type 1 may occasionally pair to form the quadrivalent *1A_s-1A_s-1A_t-1A_t*.

Genetic Criteria

As regards fertility, a general rule was formulated by Darlington (1932, ch. 7). There is an inverse correlation between the fertility of a diploid hybrid and that of its tetraploid derivative. Fertile hybrids produce sterile tetraploids; sterile hybrids produce fertile tetraploids; and hybrids of intermediate fertility give tetraploids of intermediate fertility. Autopolyploids can then be distinguished from amphiploids by the sterility of the former and the fertility of the latter.

This generalization is derived logically from the expected differences between autopolyploids and amphiploids in chromosome behavior outlined in the preceding paragraphs. The uneven segregation of homologous

chromosomes from a multivalent in an autopolyploid leads to gametic sterility. Conversely, the regular segregation of homologs from bivalents in an amphiploid leads to gametic fertility.

But we have seen that the actual chromosome behavior in polyploids often deviates from expectation. Autopolyploids with genetically determined bivalent pairing may be highly fertile. Amphiploids, on the other hand, may be sterile for various reasons. An amphiploid which forms multivalents may undergo unequal chromosome segregation, like a typical autopolyploid, and thus produce unbalanced and inviable gametes. Or the amphiploid may show good bivalent pairing, at the cytological level of observation, but the pairing is heterogenetic. The pairing partners then segregate equally as to numbers but form genetically unbalanced recombination products. The amphiploid is again gametically sterile. Or, finally, genic sterility may be intermingled with chromosomal sterility in the diploid hybrid and be carried over into amphiploid derivative.

The experimental evidence concerning the fertility of different types of polyploids is in line with the actual situation. The general rule of inverse correlation in fertility holds up in many cases but is also subject to numerous exceptions. Certainly many examples are known of autotetraploids with reduced fertility and allotetraploids with enhanced fertility. But many contrary examples are also known.

Sears (1941) produced an array of diploid hybrids and allotetraploid derivatives between ten diploid species of *Triticum*, *Aegilops*, and *Haynaldia* ($n = 7$). In 18 hybrid combinations he could compare corresponding F_1 s and allotetraploids with respect to chromosome pairing and fertility. The different diploid hybrids varied from high to low bivalent pairing. The allotetraploids showed a wide range in fertility from 100% to 0% fertility. But there was no constant relationship between the degree of pairing in the diploid F_1 and the degree of fertility in the tetraploid derivative. F_1 hybrids with low pairing may produce fertile amphiploids in some cases, or sterile amphiploids in others, depending on other contributing factors (Sears 1941).

The expected difference between autopolyploids and amphiploids in breeding behavior is also deduced from the different extreme types of chromosome behavior described earlier. An autotetraploid should show tetrasomic inheritance in characters for which it is heterozygous, whereas an amphiploid should be constant and true-breeding.

Theoretical segregation ratios in polyploids are profoundly different

from those of diploids. Let us consider a heterozygous autotetraploid with the genetic constitution $TTtt$ for a gene T located close to the centromere on four chromosomes which are distributed at random to the gametes. This heterozygote is expected to give a zygotic ratio in F_2 of 1 $TTTT$:34 heterozygotes: 1 $tttt$. If the gene T is 50 map units away from the centromere, the theoretical zygotic ratio in F_2 is 1 $TTTT$:19.8 heterozygotes: 1 $tttt$. The ratios observed in experiments fall between these two extreme types of theoretical ratios (Lindstrom 1936; Moens 1964). In any case, the homozygous recessive class occurs in a much lower frequency in F_2 under tetrasomic inheritance (between 1/22 and 1/36) than under disomic inheritance (1/4).

In contrast to this situation in autopolyploids, an allotetraploid carrying TT on one chromosome pair in genome A , and tt on another chromosome pair in genome B , is not expected to segregate for T at all.

Tetrasomic inheritance, however, is not universally present in autotetraploids or necessarily absent in allotetraploids. Tetrasomic inheritance will be exhibited by a segmental allotetraploid if there is multivalent formation. On the other hand, an autotetraploid, particularly an old one, may have undergone gene divergence so as to convert the formerly homologous alleles into separate pairs of duplicate factors.

An amphiploid may show some segregation but not in tetrasomic ratios. Suppose that we have a segmental allotetraploid with the allele pair TT on a chromosome pair in one subgenome and the allele pair tt in the other subgenome. This segmental allotetraploid will usually produce Tt gametes and $TTtt$ zygotes. But, occasionally, heterogenetic pairing (T/t and T/t), followed by independent assortment of the t alleles, will produce some tt gametes, and these can unite to give some $tttt$ zygotes. The segmental allotetraploid thus yields rare segregates toward the diploid parent carrying tt .

Gerstel and Phillips (1958) have carried out a series of ingenious experiments with synthetic amphiploids in *Gossypium* and *Nicotiana* which enable them to correlate segregation ratios with genomic affinities. Some amphiploids derived from distantly related species show no segregation. Other amphiploids formed from close relatives, like *Gossypium arboreum* and *G. herbaceum*, segregate in tetrasomic ratios. Still other amphiploids containing genomes which are well differentiated but not completely different yield rare segregates for particular marker genes (Gerstel and Phillips 1958).

Morphological Criteria

In gross morphology, finally, it is often supposed that an autopolyploid should resemble the parental diploid species, whereas an amphiploid should resemble the interspecific hybrid. But experimental autopolyploids do not always resemble the parental diploids. It is clear, moreover, that, if a segmental allopolyploid can segregate in the direction of one parental diploid for one gene, it can do likewise for other gene-determined characters as well, and eventually come to resemble a diploid species very closely in morphology and in ecology. Autoallopolyploids also tend to resemble particular diploid species in morphology.

Natural amphiploid species do, in fact, commonly vary in the direction of one or both parental diploid species. Clausen, Keck, and Hiesey (1945:150) give a list of amphiploids which have been confused taxonomically with one or both parents. The examples are repeated here in table 23.1. Many more examples have been added since 1945, and this pattern of variation can be said to be a common one (see Grant 1964a). It shows that close morphological resemblance between a given polyploid and a given diploid is not a valid criterion of autopolyploidy.

Table 23.1. Amphiploids that have been confused with one or both parents. (Clausen, Keck, and Hiesey 1945)

| Amphiploid | Confused with |
|---|--|
| <i>Spartina townsendii</i> | <i>S. alterniflora</i> and <i>S. stricta</i> |
| <i>Phleum pratense</i> | <i>P. nodosum</i> |
| <i>Poa annua</i> | <i>P. exilis</i> and <i>P. supina</i> |
| <i>Iris versicolor</i> | <i>I. virginica</i> |
| <i>Eriogonum fasciculatum</i> ssp. <i>foliolosum</i> | <i>E. f. typicum</i> and <i>E. f. polifolium</i> |
| <i>Rumex acetosella</i> | <i>R. angiocarpus</i> and <i>R. tenuifolius</i> |
| <i>Brassica napus</i> | <i>B. oleracea</i> and <i>B. campestris</i> |
| <i>Galeopsis tetrahit</i> | <i>G. speciosa</i> and <i>G. pubescens</i> |
| <i>Penstemon neotericus</i> | <i>P. laetus</i> and <i>P. azureus</i> |
| <i>Madia citrigracilis</i> | <i>M. gracilis</i> |
| <i>Artemisia douglasiana</i> | <i>A. suksdorfii</i> and <i>A. ludoviciana</i> |

Relative Frequency of Autopolyploids and Amphiploids in Nature

The identification of natural polyploids as autopolyploids or amphiploids is by no means a simple task, owing to the unreliability of the various criteria in borderline cases. Segmental allopolyploids and autoallopolyploids are likely to resemble autopolyploids in morphological characters and cytogenetic behavior. Even considerable experimental and cytogenetic work may fail to resolve the question conclusively. The problem is not impossible, however. By taking all criteria into consideration in the case of any given natural polyploid, and by resynthesizing that polyploid experimentally from its putative ancestors, it is possible to identify its nature and origin in a satisfactory manner.

The early literature on natural polyploidy can be said now, in the light of hindsight, to have oversimplified the problem. Both Darlington (1932, 1937a) and Müntzing (1936a) concluded that autopolyploids are common in nature and important in plant evolution. This conclusion was based primarily on the widespread occurrence, in numerous taxonomic species of plants, of morphologically similar diploid and polyploid forms (Darlington 1932:209; 1937a:226; Müntzing 1936a). It was supported by the evidence of multivalent formation in many of the same polyploid forms (Müntzing 1936a). But these two lines of evidence are now recognized to be insufficient to justify this conclusion.

Clausen, Keck, and Hiesey (1945) critically surveyed the evidence in some twenty-eight thoroughly investigated plant groups containing natural polyploids. For our purposes here we will pool and simplify their conclusions (from their chs. 6, 7, 8). Only three of the twenty-eight cases of natural polyploids are considered definitely to be autopolyploids, and three other cases are concluded to be probable autopolyploids. The clear-cut autopolyploids in the list are *Galax aphylla*, *Biscutella laevigata*, and *Zea perennis*; the probable autopolyploids are *Vaccinium uliginosum*, *Eragrostis palleascens*, and *Galium mollugo* and *G. verum*. The overwhelming preponderance of natural polyploids in the sample of well-investigated and critically reanalyzed cases are thus amphiploids (Clausen, Keck, and Hiesey 1945).

Stebbins (1947a) then went over part of the same ground and reduced some of the probable cases to doubtful. The only clear-cut autopolyploid remaining on the list in Stebbins' review is *Galax aphylla*.

In the ferns and fern allies, Manton (1950) found evidence pointing to the widespread occurrence of hybridization and amphiploidy. But there is little evidence in the pteridophytes for natural autopolyploidy except perhaps in *Psilotum*, according to Manton.

It is only fair to add that some more recent authors still maintain that autopolyploidy is or could be more important in nature than is indicated by the above analyses (Gilles and Randolph 1951; Darlington 1956b, 1963). In recent years the list of known amphiploids has increased greatly and the list of probable natural autopolyploids has increased slightly.

The best conclusion we can draw from the available evidence in the vascular plants is that amphiploidy is far more common and widespread than autopolyploidy. Among the few bona fide cases of natural autopolyploidy, moreover, at least some are interracial autopolyploids as, for example, *Biscutella laevigata* and *Solanum tuberosum*. Hybridity of one sort or another is thus usually present in polyploids in plants.