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Chapter 24

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CHAPTER TWENTY-FOUR

Factors Promoting Polyploidy

The question as to why polyploidy has played such an important role in plant evolution is a very complex one. It has been discussed extensively by many different authors in many different ways. Correlations have been traced between polyploidy and climate, latitude, elevation, type of habitat, life form, breeding system, hybridity, cell size, chromosome size, chromosome structure, sex chromosome mechanism, genotype, and other factors. Some of these factors are discussed in this chapter.

There is apparently no one single reason for the evolutionary success of polyploidy. On the other hand, the various polyploidy-promoting factors are not all equally important.

In attempting to analyze the evolutionary problem of polyploidy here, I have found it useful to distinguish three grades of controlling factors. They are: the primary, or most fundamental, conditions; the secondary factors, which are of considerable importance; and the tertiary, or relatively minor, factors. The conditions favoring polyploidy are presented in this order in the later sections of the chapter. By approaching the problem in this way, we can begin to put together a series of explanations.

Intrinsic Advantages of the Amphiploid Condition

It is well known that hybrids between well-differentiated races or species frequently exhibit superior vigor or viability or have enhanced physiological homeostasis. The genetic mechanisms underlying heterosis have been extensively studied and debated. It has been suggested that hybrids have a wider range of enzyme activity and a greater biochemical versatility than their parents. We are concerned here, however, not with the genetic causes but with the phenotypic results of hybridity. Heterosis and physiological homeostasis are observable features of many hybrid combinations in the animal and fungus kingdoms as well as in the plant kingdom. These heterotic and homeostatic properties of many hybrids must often be adaptively valuable to their carriers.

Now hybrids do not breed true for their heterozygous condition by the normal sexual mechanism. If sterile, the hybrid does not reproduce sexually at all. If fertile, its valuable properties of heterosis and homeostasis are lost in the later sexual generations. But amphiploidy is a genetic system which provides a way out of the impasse (Darlington 1932:chs. 13, 16). The amphiploid recovers the lost fertility, and can reproduce sexually, yet breed true for a highly heterozygous genotype. It has the advantages of internal hybridity combined with those of true breeding.

When a given natural hybrid does possess heterotic or homeostatic properties, therefore, amphiploidy is a way of perpetuating those adaptively valuable properties throughout subsequent sexual generations. Moreover, amphiploidy does not prevent segregation and recombination entirely, except in the most extreme genomic allopolyploid, but permits the release of some new variations, thereby providing an opportunity for finer adaptive adjustments to arise and become established in the later polyploid generations.

The high frequency of polyploid species in higher plants, the vast majority of which are amphiploids and the remainder of which are largely interracial autopolyploids, bespeaks the successfulness of this genetic system in perpetuating adaptive hybrid genotypes within a framework of sexual reproduction.

A second characteristic of polyploids which may be advantageous in many situations is the greater buffering in their genotypes, as compared with diploids, owing to the presence of numerous duplications. The polyploid individual is better-buffered physiologically than the corre-

sponding diploid. And it is better-buffered than the diploid in its breeding behavior, releasing its stored variability more slowly owing to tetrasomic inheritance. These buffering properties are true of autopolyploids as well as amphiploids.

Modes of Formation

The two main modes of origin of the polyploid condition are somatic doubling in mitosis and nonreduction in meiosis (Heilborn 1934).

In somatic doubling the chromosomes divide during mitosis, but do not separate to the poles, and are all included in one daughter nucleus. As a result, a $2n$ somatic cell gives rise to a $4n$ daughter cell. This somatic doubling may affect certain particular vegetative tissues which are not in the line of development to flowers, such as the root nodules in legumes, in which case the process does not concern us further here. Somatic doubling may also take place in the zygote or early embryo and change the whole plant. Or it may occur in a bud and consequently affect one branch of the plant. Tetraploid *Primula kewensis*, which we discussed briefly in chapter 19, arose by somatic doubling of particular flowering branches on the diploid hybrid plant.

Nonreduction involves the failure of cell wall formation during meiosis. When this occurs in diploid pollen mother cells and embryo sac mother cells, diploid spores and gametes are formed. Tetraploid zygotes may then arise in one step after union of two unreduced gametes. This was the mode of origin of *Raphanobrassica*, as noted in chapter 19.

Or the nonreduction may occur in one germ line at a time to give rise to either diploid pollen grains or diploid eggs. A new tetraploid individual can then develop in two steps. In the first step a $2n$ and $1n$ gamete give a $3n$ zygote, and in the next generation an unreduced $3n$ gamete fuses with a normal $1n$ gamete to produce the tetraploid. Artificial *Galeopsis tetrahit* arose in such a sequence of separate steps, as we saw in chapter 19.

A less common mode of origin of the polyploid condition is polyspermy, or the fertilization of an egg by two male nuclei. This process has been reported in *Listera ovata* and some other orchids (Hagerup 1947).

Amphiploids usually arise from diploid hybrids, as in the examples of *Primula kewensis* and *Raphanobrassica*. It has also been suggested that,

in certain groups, particularly in *Zauschneria* and *Galium*, amphiploids have originated as products of hybridization between specifically distinct autopolyploids (Clausen, Keck, and Hiesey 1945). In such cases, if this is the correct interpretation, the doubling process occurred first and the hybridization took place later.

Polyploidy and Life Form

Müntzing (1936a) surveyed the chromosome numbers in 48 herbaceous genera of angiosperms containing both perennial and annual species. He found a correlation between chromosome number and growth habit. As a general rule, the perennial species of a genus have a higher chromosome number than the annuals in the same genus. In many cases the higher chromosome numbers in the perennial species are clearly of polyploid origin. Thus we find polyploid perennials and diploid annuals in *Helianthus*, *Zea-Euchlaena*, *Sorghum*, and other genera (Müntzing 1936a).

Stebbins (1938) confirmed and extended this finding in a subsequent survey of 202 genera of dicotyledons. He tabulated chromosome numbers in each of three life-form classes, namely, woody plants, perennial herbs, and annual or biennial herbs. A high frequency of polyploid species is found in 52% of the herbaceous genera and in 36% of the woody genera. Hence the tendency for polyploidy is stronger in the herbaceous dicotyledons. And, when the sample of herbaceous genera is broken down into perennial vs. annual subsamples, the tendency for polyploidy is clearly stronger in the perennial fraction (Stebbins 1938).

Gustafsson also found that the frequency of polyploidy is statistically higher in the perennial members than among the annual members of the Gramineae, Ranunculaceae, Cruciferae, Leguminosae, and Compositae in northern Europe (Gustafsson 1946–1947, ch. 15). It can be noted that the pteridophytes in which Manton (1950) found such a high frequency of polyploidy are predominantly herbaceous perennials.

Müntzing's (1936a) way of explaining the observed correlation between polyploidy and perennial herbaceous habit was to suggest that the polyploid condition influences the life form. He pointed out that experimental autopolyploids generally have a slower growth rate than the parental diploids. This retardation of growth would, in many cases, convert

an annual into a perennial on chromosome doubling (Müntzing 1936a; also Randolph 1935).

Later authors have preferred to trace the connection in the opposite direction. The perennial growth habit, with the possibility of vegetative propagation, favors polyploidy (Stebbins 1938; Gustafsson 1946–1947, 1948; Darlington 1956a, 1963). This interpretation of the facts is strongly supported by a correlation noted by Darlington. One of the very few natural polyploids in the conifers, *Sequoia sempervirens*, is also one of the exceptional conifers which regenerates from suckers (Darlington 1956a).

In what way does vegetative propagation favor polyploidy? This question is answered in different ways by different authors. Vegetative propagation favors the survival of polyploid types which have already arisen, according to Darlington (1963:60). Clonal reproduction reduces normal recombination but facilitates the functioning of unreduced gametes, according to Gustafsson (1946–1947 ch. 15).

A simpler and probably more general explanation is that the long life span of a perennial herb, and especially one with means of vegetative propagation, gives a hybrid plant greatly enhanced chances of undergoing somatic doubling (Stebbins 1938; Grant 1956c). The perennial herbaceous hybrid *Primula kewensis* did not produce fertile tetraploid branches in its first year of existence, though it did so on three separate occasions in later years, and it is fair to assume that this hybrid might never have given rise to fertile amphiploid derivatives if it had had a short life span.

Primary Factors

Three important generalizations about the nature and distribution of polyploidy have now been established. First, polyploidy is a characteristic feature of the plant kingdom, and of this kingdom only, and here it occurs predominantly in long-lived perennial herbs. Second, polyploidy in plants usually takes the form of amphiploidy. And, third, amphiploidy is a genetic system for perpetuating an adaptively valuable hybrid genotype by means of sexual reproduction. Indeed, it is probably the best possible genetic system for accomplishing this difficult task. With these generalizations before us to serve as a guide to our thinking, we can now define the primary polyploidy-promoting factors.

Polyploidy is promoted by a combination of three *primary* factors. These are: (1) long-lived organisms usually possessing means of vegetative propagation; (2) primary speciation accompanied by chromosome re-patterning; and (3) the common occurrence of natural interspecific hybridization. These three factors have been discussed as phenomena in themselves, and without special reference to polyploidy, in previous chapters of this book.

It is important to recognize that polyploidy, as a common and widespread evolutionary development, depends on the joint action of all three factors. Any single factor, if lacking in any given group of organisms, will greatly retard or completely prevent the formation of polyploid species. Factors 2 and 3 are especially critical. Factor 1 is important but not indispensable and, where absent in annual herbaceous groups, can be compensated for by other secondary factors, as we shall see later.

The three primary factors occur characteristically and distinctively in the higher plants. And it is here also that polyploid species have evolved frequently and extensively. The same three factors are largely wanting or exceptional in the animal kingdom, where polyploidy is a very rare condition. The fundamental differences between higher plants and higher animals have thus led to fundamental differences in their respective patterns of evolution, as Gustafsson (1946–1947 ch. 15) pointed out, and one of those differences is the occurrence of polyploidy.

Within the plant kingdom, polyploidy has an uneven distribution which can be correlated in many cases with the presence or absence of one particular primary factor.

Polyploidy is largely absent in plant groups conforming to the *Ceanothus* pattern of speciation. Examples in *Quercus*, *Ribes*, *Ceanothus* and other angiosperm genera were described in chapter 11. Khoshoo (1959) pointed out that many non-polyploid genera occur in the conifers. These are all woody plants which have long individual lives and often reproduce vegetatively. Natural hybridization is frequent. But the related hybridizing species do not differ with respect to chromosomal rearrangements (Khoshoo 1959). In short, factors 1 and 3 are present, but factor 2 is absent.

Müntzing (1936a) showed that polyploidy was definitely less frequent in annual herbs than in perennial herbs belonging to the same genus. Heiser (1950) found that polyploidy is relatively uncommon in the weed flora of Indiana and showed that this is correlated with the prevalence of

an annual life cycle in successful weedy plants. Gustafsson (1946–1947, 1948) has also pointed out that annuals in general, and weed floras composed chiefly of annuals in particular, have a low percentage of polyploid species.

Now annual herbaceous plants belonging to the *Madia* pattern of species relationships are characterized by interspecific differences in chromosome structural arrangement. Natural hybridization is again common. But the individual organisms are short-lived and lack means of vegetative reproduction. Factors 2 and 3 are present, but not factor 1.

Latitude and Altitude

It has long been known that the frequency of polyploidy in higher plants is correlated with latitude. The percentage of polyploid species within a regional flora increases regularly from lower to higher latitudes. This trend was first pointed out by Hagerup (1932) and Tischler (1935). The early data were subject to various errors which were eliminated in later studies without changing the general conclusion (Tischler 1955).

The early surveys have also been greatly extended by more recent studies. The regional floras cited in the earlier papers have been restudied more completely, and new regional floras have been added to the sample. The individual studies are too numerous to list here; reviews with numerous references are given by Löve and Löve (1949, 1957) and Hanelt (1966). The newer evidence confirms the older generalization.

Table 24.1 gives the percentage of polyploid angiosperms in a series of regional floras ranging from 36° to 84° north latitude in Eurasia and the Arctic. The data are taken and condensed slightly from papers by Löve and Löve (1957) and Hanelt (1966), which can be consulted for further details. The regional floras listed in the table have all been thoroughly studied cytotaxonomically. The floras are arranged in order of increasing latitude in the table. It will be seen that the frequency of polyploid species ranges from 37% in the Mediterranean region to 74% in Spitsbergen in a transect through Europe, and is generally high throughout arctic and subarctic zones (Löve and Löve 1949, 1957; Löve 1953; Tischler 1955; Hanelt 1966).

The most recent estimate of the frequency of polyploid species in the

Table 24.1. Frequency of polyploid species of angiosperms in different latitudinal zones in Eurasia and the Arctic. (condensed from Löve and Löve 1957; and Hanelt 1966)

Area	Latitude N°	Polyploids, %
Sicily	36–38	37.0
Rumania	44–47	46.8
Hungary	46–49	48.6
Pardubice, CSR	50	52.3
Central Europe	46–55	50.7
Schleswig-Holstein	54–55	54.5
Denmark	54–58	53.5
England	50–61	52.8
SW Greenland	60–62	74.0
Faroës	62	71.0
Iceland	63–66	71.2
Sweden	55–69	56.9
Finland	60–70	57.3
Norway	58–71	57.6
NW Alaska	68	59.3
Devon Island	75	76.0
Spitsbergen	77–81	74.0
Franz Joseph Land	80–82	75.0
Peary Land	82–84	85.9

vascular plant flora of the arctic region as a whole is 60% in the low arctic and 70% in the high arctic (Löve and Löve 1975).

The frequency of polyploids also increases with latitude on the Pacific coast of North America from California to Alaska (Stebbins 1971:185). There is some evidence to indicate that the same trend toward increasing proportion of polyploids at higher latitudes occurs also in the southern hemisphere (Hair 1966; Hanelt 1966).

The frequency of polyploid species tends to be relatively high in high mountains. Hanelt (1966) gives percentage figures ranging from 45 to 85% polyploids in various high montane floras of Eurasia, the Americas, and New Guinea. The polyploids sometimes have a higher frequency in high mountains than in the neighboring lowlands, but this is not always the case (Hanelt 1966).

Löve and Löve (1967) have compared neighboring alpine and forest floras on Mt. Washington in the White Mountains of New Hampshire with respect to incidence of polyploidy. In the alpine zone above tree-line, 63.6% of the taxa of vascular plants are polyploid, whereas the surrounding forest vegetation has only 45% polyploids. The frequency of

polyploidy is thus significantly higher in the alpine zone (Löve and Löve 1967).

The facts are straightforward enough. But what do they mean? A variety of interpretations have been put forward. In order to show the variety, I will list the suggested explanations below in synoptical form. Good discussions are given by Löve and Löve (1949, 1953), Stebbins (1950, 1971), Johnson, Packer, and Reese (1965), and Hanelt (1966).

1. Severe cold climates induce polyploid formation by means of temperature shocks (Hagerup 1932).

2. Polyploids are better adapted to cold climates and to the associated environmental conditions in cold regions than are diploids (Löve and Löve 1949, 1967; Löve 1953).

3. The correlation between polyploidy and latitude or altitude is an indirect one. Polyploidy is most frequent in perennial herbs with vegetative reproduction, and this life form is prevalent in arctic and alpine floras (Gustafsson 1946–1947, 1948).

4. Pleistocene climatic changes, including the advance and retreat of ice sheets and glaciers, bring about changes in the distribution of the existing species. New contacts are made, natural hybridization occurs, and hybrid polyploids are formed (Manton 1950).

5. The Pleistocene climatic and topographic changes promote natural hybridization in new combinations as stated above. The retreat of the ice then opens up new habitats for colonization. Amphiploids are particularly well suited to colonize these new open habitats (Stebbins 1950, 1971; Ehrendorfer 1965).

Explanation 1 is no longer regarded as viable. The crucial stage is the establishment, not the formation, of polyploid types in statistical comparisons between whole floras. Explanation 3 can also be set aside now. The correlation between polyploidy and latitude holds true within the life-form class of perennial herbs in the various floras (Löve and Löve 1949).

The remaining explanations, which are all plausible, cannot be evaluated on the basis of the statistical and floristic evidence presented so far. More detailed approaches are needed.

Ecological Factors

One approach to the problem outlined above is to study the frequency of polyploids in different ecological facies of a given northern flora.

Johnson and Packer (1965) obtained data on the frequency of polyploid angiosperms in different parts of a valley in northwestern Alaska at 68° N latitude. The polyploid frequencies varied widely between different habitats in the same valley. Polyploids were much more frequent in disturbed habitats with wet soils and shallow permafrost than in more stable habitats with drier soils and deeper permafrost.

Ehrendorfer (1980) surveyed different plant communities in the flora of lower Austria from the standpoint of polyploid frequency. The highest proportion of polyploid species is found in meadows, which are recent products of human activities in this area, whereas forest communities have lower polyploid frequencies.

A second approach to the problem is to make detailed studies of the geographical and ecological distribution of related diploid and polyploid species within particular plant groups.

A common pattern in both the angiosperms and the ferns is this: the polyploid members of a group are widespread while their diploid relatives have more narrow distributions (Stebbins 1950:347; Manton, 1950). In the fern genera *Cystopteris*, *Polypodium*, *Dryopteris*, and *Asplenium* the polyploids are abundant but the diploids are either rare, relictual, or extinct (Manton 1950). An angiosperm group with a parallel difference between polyploids and diploids is the *Biscutella laevigata* group (Cruciferae) (Manton 1934, 1937).

The *Gilia inconspicua* complex (Polemoniaceae) contains numerous diploid and tetraploid species in the deserts and mountains of western North America. In this group the diploid species are generally restricted geographically and ecologically as compared with their amphiploid derivatives. Many of the diploid species are definitely relictual. The tetraploid species, on the other hand, are wide-ranging and abundant through large and diversified territories (Grant 1964a). The tetraploid *Gilias* are also definitely more vigorous than their diploid relatives in cultivation in the experimental garden.

The evidence from the two approaches described in this section favors explanations 4 and 5. But the evidence is not conclusive and the problem is still open.

My view, colored by my own personal experience with several groups of polyploids and diploids in both nature and the experimental garden, is that amphiploids do often exhibit superior vigor, homeostatic buffering, and adaptability as compared with their diploid relatives. These features

would often give the amphiploids an adaptive superiority over the ancestral diploids in nature. The opening of new habitats for colonization in the ancestral territory, as a result of climatic, human, or other disturbances, provides the ecological opportunity in which the amphiploids can exploit their inherent advantage.

Polyploidy and the Breeding System

The main mode of origin of amphiploids in annual plants is nonreduction followed by union of the unreduced gametes (Clausen, Keck, and Hiesey 1945). If the annual hybrid plant has an outcrossing breeding system, the chances of union of two unreduced gametes are very slight. This hybrid may initiate introgression but is unlikely to produce an amphiploid during its short life span. But if the annual hybrid plant is autogamous, the chances of two unreduced gametes uniting are much more favorable (Grant 1956c).

Two annual sections of the genus *Gilia*, the sections *Gilia* and *Arachnion* ($x = 9$), contain a total of 39 species, all but one of which have been studied cytotaxonomically and genetically. As to ploidy in the 38 cytologically known species, there are 23 diploids, 14 tetraploids, and 1 octoploid (Grant 1959, 1964a, 1965, for the basic data). The same species also range in breeding system from obligate outcrossers to autogamous inbreeders. It is significant that all of the 15 polyploid species are autogamous (Grant 1956c). There is one exceptional outcrossing race in one otherwise autogamous tetraploid species.

The ancestry of the amphiploid species of annual *Gilia* has been traced back in a number of instances to particular autogamous diploid species. Conversely, the autogamous diploid *Gilias* have produced proportionately more amphiploids than have the cross-fertilizing diploid *Gilias*.

The same correlation between autogamous breeding system and polyploid constitution is found in the annual sections of various other genera. A majority of the polyploid species in the annual members of *Galeopsis*, *Madia*, *Microseris*, *Clarkia*, *Mentzelia*, *Amsinckia*, and *Escholtzia* are autogamous (Grant 1956c). The observed correlation is in agreement with the idea that autogamy is a polyploidy-promoting factor of secondary importance which compensates to some extent for the short individual life span in annual plants.

Perennial herbs, in which polyploidy is common, are usually outcrossing and often self-incompatible. The correlation between the three conditions—growth habit, polyploidy, and breeding system—can be explained in different ways in this case.

Gustafsson (1946–1947), following Lewis (1943b), suggests that the style in a self-incompatible diploid acts in such a way as to favor the functioning of unreduced pollen grains produced by the same plant, thus leading to the formation of tetraploid or at least triploid zygotes. In my opinion a simpler and more direct explanation is quite sufficient. Hybrid plants with a perennial habit have a long time, and hence a fair chance, of undergoing polyploid doubling, usually by somatic doubling, but also sometimes by the union of unreduced gametes. In Gustafsson's view, then, the causal connection is between self-incompatibility and polyploidy, and perenniality is a correlated condition; whereas in my view the causal connection is between perenniality and polyploidy, and outcrossing is the correlated condition.

There is another angle to this question. Polyploidization converts a self-incompatible diploid into a self-compatible tetraploid in plants with the *Nicotiana*-type or gametophytic system of self-incompatibility (Lewis 1943a, 1966). In *Solanum* and *Nicotiana* within the Solanaceae and in some members of the Scrophulariaceae and Leguminosae, the diploid species tend to be self-incompatible and the natural polyploid species self-compatible (Lewis 1966).

Muller (1925) suggested that the establishment of a polyploid condition would be particularly difficult in dioecious organisms. One of the main reasons for this was supposed to be the breakdown of the sex-determining mechanism in tetraploids with the constitution XXYY for the sex chromosomes. Muller (1925) offered this suggestion in the hope that it would account for the rarity of polyploidy in animals, which are mostly dioecious, and its common occurrence in plants, which are mostly hermaphroditic.

Muller's hypothesis has been partly confirmed and partly not confirmed by the subsequent factual evidence. The few bona fide examples of polyploidy in animals are in fact found in groups which are either parthenogenetic (brine shrimp, sowbug, bagworm moth, *Otiorrhynchus* weevil, *Ochthiphila* fly) or hermaphroditic (earthworms) (Bungenberg, 1957; Stalker, 1956). On the other hand, the polyploid condition has succeeded in establishing itself in some dioecious groups of plants in both

nature (*Salix*, *Rumex*, *Galium*) and experiment (*Melandrium*) (Westergaard 1940; Löve 1944; Stebbins 1950:367; Dempster and Ehrendorfer 1965).

The Influence of Chromosome Size

The mechanics of chromosome and cell division probably acts as a limiting factor on polyploidy, as Darlington suggested long ago. Reciprocal relationships exist between cell size, chromosome size, and polyploid chromosome numbers (Darlington 1932:204 ff.; 1937a:84).

It is known that autopolyploids often have a slower growth rate than the related diploids, owing in part at least to retarded cell division (Müntzing 1936a). At some ploidy level, which differs from one plant group to another, the artificial polyploid crosses a viability threshold, which again is determined partly by mitotic conditions (see chapter 22).

The cells forming nutritive tissues in embryo sacs and anthers often or usually contain endopolyploid nuclei. The cell is a product of repeated endomitotic divisions; it does not undergo cell division. Such endopolyploid cells attain ploidy levels far above those found in whole plants. Antipodal cells in the embryo sacs of certain members of the Ranunculaceae, Papaveraceae, and Compositae may be as high as 64-ploid (Müntzing 1961:320). The record is held by 4096-ploid nuclei in the embryo sac of *Phaseolus coccineus* (= *P. multiflorus*) (Darlington 1965:670).

Individual cells which do not have to divide can clearly function at much higher ploidy levels than whole plants which must grow by cell division. This difference between terminal members of cell lines and growing plant bodies as regards tolerance of high ploidy levels is in line with Darlington's hypothesis.

The exigencies of cell mechanics may account for the absence or rarity of polyploidy in some Lilaceae and in some woody plants. *Lilium*, *Fritillaria*, and some other lilaceous genera with large chromosomes either have no polyploids or no high polyploids. It is possible that the chromosomes are too large for cell division with high polyploid numbers in such cases (Darlington 1932:477, 1937a:84).

In woody dicotyledons the narrow cambium cells must restrict both chromosome number and chromosome size. The relatively low frequency

of polyploidy in woody dicotyledons compared with perennial herbaceous dicotyledons, and the complete absence of polyploidy in some dicotyledonous genera and families, may be a result of the bottleneck of cambium cells (Darlington 1937a:84; Stebbins 1938).

The Influence of the Genotype

Reduced chromosome pairing in a species hybrid sets the stage for nonreduction and amphiploid formation. Reduced pairing is a result of chromosomal rearrangements between the parental genomes. But chromosome behavior in meiosis is also under the control of specific genes, as numerous studies have shown (Darlington 1937a, 1965; Riley 1960; Rees 1961; Lewis and John 1963; Waines 1976). It follows that the frequency of non-reduction and hence of polyploid production in an array of chromosomally sterile hybrids may be affected by genotypic differences with respect to particular meiotic genes (Swietlińska 1960; Swietlińska and Zuk 1965; Grant 1965).

Genes controlling various aberrations of meiosis, such as asynapsis or abnormal spindle formation, are known in maize, *Drosophila*, and other genetically well-known organisms. Meiotic genes with the particular effect of interest to us here, namely the failure of the second meiotic division, so as to produce unreduced gametes, have been found in *Datura stramonium* and *Zea mays* (Satina and Blakeslee 1935; Avery, Satina, and Rietsema 1959; Rhoades and Dempsey 1966).

A recessive mutant gene in *Datura stramonium* known as "dyad" causes dyads of unreduced spores to be formed at the end of meiosis in both the male and female lines. A diploid *Datura* plant homozygous for "dyad," when selfed, gave rise to some tetraploid progeny (Satina and Blakeslee 1935; Avery, Satina, and Rietsema 1959). Plants of *Zea mays* carrying the recessive allele of "elongate" in homozygous condition produce some unreduced eggs but normal haploid pollen. The first-generation progeny of "elongate" plants therefore consist mainly of triploids. These can go on to yield tetraploids and higher polyploids in subsequent generations (Rhoades and Dempsey 1966).

The diploid F₁ hybrid of *Rumex thyrsoiflorus* × *acetosa* shows individual variation in meiotic behavior. Some F₁ plants have normal meiosis and produce tetrads; others lack the second division and produce dyads

of unreduced gametes. The segregation of dyad-forming types occurs also in the F₂ and B₁ generations. The F₂ progeny of hybrid individuals with normal meiosis are diploid ($2n = 14$). But the F₂ progeny of dyad-forming hybrid plants are tetraploids or near-tetraploids with $2n = ca. 25$ (Swietlińska 1960; Swietlińska and Zuk 1965).

Eight species of Leafy-stemmed *Gilias* have been intercrossed artificially to produce 15 hybrid combinations which have reached the stage of flowering. Four of the 15 classes of interspecific hybrids have doubled spontaneously by the union of unreduced gametes to yield fertile or semi-fertile amphiploid progeny in F₂. The four amphiploid-producing hybrids all have *Gilia millefoliata* and/or *G. valdiviensis* as one or both parents. *Gilia millefoliata* and *G. valdiviensis* are two closely related diploid ($2n = 18$) species belonging to the same genome group. There is thus an unusual concentration of the *millefoliata* genome in the sample of artificial spontaneous amphiploids in the Leafy-stemmed *Gilias* (Grant 1965).

One of the hybrids, *Gilia millefoliata* × *achilleaeifolia*, doubled repeatedly in three replicate cultures. Replicate cultures of other hybrid combinations not containing *G. millefoliata* or *G. valdiviensis*, by contrast, have consistently failed to yield amphiploids (Grant 1965). It is significant in the light of these experimental results that two of the three known natural tetraploid species of Leafy-stemmed *Gilia* carry the *millefoliata* genome (Grant 1965).

Levin (1968) finds a similar situation in the genus *Phlox* in eastern North America. There are five allotetraploid species of *Phlox* in this area. Four of the five tetraploid species contain the genome of the diploid species, *Phlox pilosa* (Levin 1968).

It appears, therefore, that parental species differ genotypically in their ability to produce amphiploid progeny, in the experimental plot and in nature, where other factors are more or less equal. The genic contents of different genomes may be a tertiary factor affecting the systematic distribution of polyploids within a genus or section composed of diverse, sympatric, basic species.

Conclusions

Polyploidy is a common and widespread genetic system in higher plants. Within the subkingdom of vascular plants the polyploid condition

is unevenly distributed with respect to systematic relationships, life form, climate, breeding system, chromosome structure and size, and other factors. The clue to the reasons for the evolutionary success of polyploidy in higher plants lies hidden in these various correlations and can be revealed by a proper analysis.

The vast majority of the naturally occurring polyploid species of plants that have been analyzed taxogenetically have turned out to be amphiploids. Now amphiploidy is a type of permanent hybridity. It is a genetic system which permits a species hybrid to bypass the sterility barrier and to breed true for its hybrid constitution. Amphiploidy is a genetic system enabling plants to exploit the intrinsic advantages of a highly heterozygous genotype, particularly heterosis and physiological homeostasis, in the numerous hybrid combinations where these advantageous properties are present.

The ability of a plant group to take advantage of the amphiploid genetic system in its evolutionary development depends on factors of various sorts and various degrees of importance. There are factors affecting the origin of a new polyploid and other factors affecting its subsequent establishment as a natural population. Internal and external factors are involved in both the origin and the establishment of the new polyploid.

Of primary and fundamental importance is a combination of three conditions. The first one is the existence of diploid species carrying different genomes or subgenomes. The second is natural hybridization between these species. The third is a long-lived perennial growth habit to increase the chances of somatic doubling; or, as a partial compensation in short-lived annuals, an autogamous breeding system to increase the chances of union of unreduced gametes. If any one of the three conditions is lacking in any given plant group, polyploidy is expected to be absent or rare. A survey of the distribution of polyploidy in relation to chromosome repatterning, hybridity, and perennial growth habit (or autogamy as a substitute in annuals) shows that polyploidy is, in fact, common only in plant groups possessing these characteristics.

Polyploidy is not uniformly present or uniformly common in all plant groups meeting the three primary conditions. The uneven distribution of polyploidy among plant groups which are comparable with respect to the primary factors points to the existence of other secondary and tertiary factors.

Disturbed habitats and stressful environments, often in cold climates,

are among the external factors of secondary importance that favor polyploidy. Chromosomes which are large in relation to cell size, and cells which are small in relation to chromosome size and numbers, are among the internal secondary polyploidy-inhibiting factors. The presence or absence of genes causing failure of the second meiotic division and hence the formation of unreduced gametes is a tertiary factor which may explain the proportionately unequal contributions of different diploid species to the production of amphiploids within some genera.