

CHAPTER IX

Polyploidy II: Geographic Distribution and Significance of Ployploidy

THE FACT that polyploid species may have different geographic distributions and ecological preferences from those of their nearest diploid relatives has been noted by a number of authors. There has, however, been no unanimity of opinion on the effects of polyploidy on distribution, and a number of different tendencies have been noted. The principal ones of these are as follows.

Hagerup (1932) first brought out the concept that polyploids are more tolerant of extreme ecological conditions than their diploid relatives, and he illustrated it with examples taken from the desert flora of Timbuktu, in northwestern Africa. The most striking of these examples is in the grass genus *Eragrostis*, in which Hagerup found three species: a diploid annual of lake margins, *E. cambessedesiana*; a tetraploid perennial, *E. albida*, found in somewhat drier places; and a robust perennial octoploid, *E. pallescens*, found on the very dry sand dunes. Hagerup believed these to form an autopolyploid series, based on Hitchcock's study of their external morphology. But the hazards of determinations of the type of polyploidy on such evidence have already been pointed out, and these are particularly great in a genus like *Eragrostis*, which is even for the grasses very poor in diagnostic characteristics for the separation of species. Furthermore, the large number of African species of this genus is almost unknown cytologically and completely unknown in respect to the behavior of the chromosomes at meiosis. *Eragrostis*, therefore, would seem at present to be a particularly unfavorable example on which to base any generalizations about polyploidy and distribution or ecological preferences. Based on the example of *Empetrum*, which contains a diploid, *E. nigrum*, in northern Europe, and a tetraploid, *E. hermaphroditicum*, in Greenland, Hagerup sug-

gested that polyploidy might be associated with the severe cold of arctic regions. But in later papers (1933, 1940), the same author cited two examples, *Vaccinium uliginosum* and *Oxycoccus microcarpus*, in which diploid representatives of the species as ordinarily recognized by systematists have a more northerly distribution than tetraploids referred to the same species. All three of these examples are believed by Hagerup to be autopolyploid series, but in each one he studied only the European and Greenland representatives of groups which have their centers of distribution on the North American continent, and in none of them was cytological or genetic evidence obtained as to the nature of the polyploidy. All, therefore, suffer from incompleteness of the data, but, in the example of *Oxycoccus*, Camp (1944) has produced some evidence that the tetraploid is either an allopolyploid or at least an intersubspecific autopolyploid which owes its characteristics to gene combinations derived from two ecologically different types, the high arctic *O. microcarpus* and the temperate American *O. macrocarpus*. *Campanula rotundifolia* (Böcher 1936) is another European tetraploid which has a diploid relative in the high arctic regions.

The hypothesis of Hagerup, that the frequency of polyploids in regions with a severe climate is due to the direct action of the environment in inducing failure of meiosis in the sex cells, was examined by Gustafsson (1948) through a study of the frequency of polyploids in a particularly severe locality, the Dovre massif of the Norwegian mountains, in which the snow does not melt until late summer. Here the proportion of polyploids among sexual species was actually lower than the average for the Scandinavian mountains, and not appreciably higher than in lowland plants of this country.

That polyploid is favored by existence along the seacoast was concluded by Shimotomai (1933), on the basis of his studies of *Chrysanthemum* in Japan, and by Rohweder (1937), after studying the Darss-Zingst area, in northern Germany. But in the genus *Artemisia*, Clausen, Keck, and Hiesey (1945a) have shown that in the complex of *A. vulgaris* in western North America the coastal species, *A. suksdorfii*, is diploid, the widespread desert species, *A. ludoviciana*, is tetraploid, while the hexaploid *A. douglasiana* grows in the most favorable habitats of all three species,

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namely, the valleys and coastal hills of California and Oregon. Tischler (1937) found a high percentage (65 percent) of polyploids in the halophytic flora of certain islands in the North Sea, and from that concluded that polyploidy is associated with adaptation to the severe conditions of saline habitats. This conclusion was apparently supported by the data of Wulff (1937a) on the halophytic flora of Schleswig-Holstein, but Tarnavski (1939) found only 26 percent of polyploids among 38 halophytic species of the east coast of Rumania. Sokolovskaya and Strelkova (1940) found 50 percent of polyploids in the alpine flora of the Caucasus, but in the corresponding floras of the Pamirs and the Altai Mountains of central Asia, which have more extreme climates, the percentages of polyploids were, respectively, 65 percent and 85 percent. From this they concluded that polyploidy is causally related to the tolerance of these extreme climatic conditions. But Bowden (1940), after obtaining the chromosome numbers of a considerable number of species of flowering plants from various countries, which were growing under cultivation in Virginia, found no correlation between the incidence of polyploidy and the winter hardiness of the species.

One of the most widely known studies of the relation between polyploidy and distribution is that of Tischler (1935), in which he reported that among four different European floras studied by him the lowest percentage of polyploidy was found in the most southerly one, that of Sicily, with only 31 percent of polyploids. Schleswig-Holstein, in northern Europe, was found to have 44 percent of polyploids, while two more northerly localities, the Faroe Islands and Iceland, were reported as having still higher percentages of polyploids, the figures being 49.4 percent and 54.5 percent, respectively. In a more recent publication (Tischler 1946), the percentage of polyploids on the Greek Islands of the Cyclades was found to be about the same as in Sicily (34 percent). Tischler's results have been criticized on the ground that many of his counts were based, not on plants found in the region for which the species was scored as diploid or tetraploid, but on records in the literature for the species concerned. Such records are hazardous, because many species have diploid and polyploid races with different distributions. However, both Tischler and Wulff (1937b) later made counts on numerous species from

Schleswig-Holstein, and their more complete data were reported, along with those for many other localities in northern Europe as well as the Faroes, Iceland, and Spitzbergen, by Löve and Löve (1943). The data for the extreme conditions and very poor flora of Spitzbergen were first reported by Flovik (1940). The values reported by Löve and Löve were higher for all localities than those given by Tischler, and the percentage recorded for Spitzbergen, 77 percent, was by far the highest of all. But the gradient of increasing polyploidy northwards was the same. The statistical significance of all their differences was found by Löve and Löve to be very high when floras from different latitudes were compared. All these authors showed that the percentage of polyploids is from 19 to 32 percent higher among monocotyledons, which in these floras consist mainly of Gramineae and Cyperaceae, than it is among dicotyledons.

The apparently greater percentage of polyploids in higher latitudes and higher altitudes than in regions with milder climates is attributed by both Tischler and Löve and Löve, as well as by Müntzing (1936), to the greater hardiness of the polyploids, although Löve and Löve suggest also that the greater tolerance of autopolyploids to the photoperiodic conditions of long days may be an additional factor. The assumption of a greater hardiness in polyploid species is criticized by Bowden (1940), Nielsen (1947), and Gustafsson (1947c, 1948), chiefly on the grounds that when diploids are compared with their most nearly related auto- or allopolyploids the greater hardiness of the polyploids is by no means consistently present. The same fact was noted by Clausen, Keck, and Hiesey (1940, 1945a) for the western American species of the genera *Zauschneria*, *Achillea*, and *Artemisia*. Gustafsson has pointed out sources of error in comparisons of percentages of polyploidy based on studies of entire floras. The percentage of polyploids varies greatly from one family to another, being particularly high in the Gramineae, the Cyperaceae, and the Rosaceae. Hence, if a particular flora happens to possess an unusually high percentage of species of one or more of these families, it will automatically have a higher percentage of polyploids than floras which have lower percentages of them. Furthermore, as was demonstrated by Müntzing (1936) and Stebbins (1938b), the highest percentage of polyploids is to be found in perennial herbs, while annuals

and woody plants have lower percentages of polyploidy. High percentages of polyploidy are, therefore, to be expected in floras containing a great preponderance of herbaceous perennial species, as is the case in most cool temperate and subarctic floras (Raunkiaer 1934), while, conversely, floras like those of the Mediterranean region, which are rich in woody plants and annuals, can be expected to contain a relatively low percentage of polyploids.

These sources of error can be overcome only by studying the problem of polyploidy and distribution not from the point of view of entire floras, which may contain a very large or a small percentage of diploid species which are nearly or quite incapable of forming successful polyploids regardless of the climatic conditions to which they are exposed, but through analysis of a series of species groups containing polyploids which are known or suspected on the basis of good evidence to be derived directly from the diploid species with which they are compared. Until recently this approach has been impractical because of the small number of polyploid complexes which were sufficiently well known. Before a group can be safely subjected to distributional analysis, the entire world distribution of its members must be known, and direct or indirect evidence on the actual or probable chromosome numbers of its members must be available at least for representative localities throughout its range.

By searching the literature on polyploidy, the writer has assembled 100 examples of such groups (genera, subgenera, or sections of genera) which are at least well enough known so that they can be used tentatively for the type of comparison needed. The list is too long to reproduce here, but some features of it may be mentioned, and the principal conclusions drawn from it will be summarized. In the first place, all the examples are of groups confined to the temperate and arctic floras of the northern hemisphere. No tropical or Southern Hemisphere groups are known well enough for this purpose. Nearly one half (46) of the groups occur to a large extent in the regions covered by the Pleistocene glaciation. Twenty-one are Holarctic in distribution, 56 are North American, and 23 are of the Old World. Nearly all of the latter are European, while of the North American examples two are essentially northern, 21 eastern, and 33 western. The sample, therefore, is by no means a random one, and it reflects

both the amount of cytotaxonomic study which has been done in the various regions and the degree to which the present writer is familiar with their floras.

The principal results are as follows. In 60 of the 100 examples, the polyploids as a group have a wider distribution than their diploid ancestors, in seven the area of diploids and polyploids is about equal, and in 33 the polyploids occupy a smaller area. There exists a tendency, therefore, for polyploids to have wider geographic ranges than their diploid ancestors, but this tendency is by no means universal. There was no difference in this respect between the groups found in glaciated regions and those outside of the areas covered by the Pleistocene ice. When the geographic position of the diploids was compared with that of the polyploids, the largest number of examples (31) was found to be those in which, as in *Zauschneria* and *Biscutella*, the diploids are distributed about the periphery of the range of the group as a whole, and the polyploids occupy the central portion. However, the number of examples (28) in which the diploids are centrally located, as well as of those (27) in which the diploids are more southern and the polyploids more northern in distribution, are both only slightly, and probably not significantly, smaller. In seven examples the diploids have a more northerly distribution than the polyploids, while in the remaining seven the distribution is of another nature or not noticeably different between diploids and polyploids.

These results indicate that no general rules can be formulated to govern the relation between the distribution of diploids and tetraploids, at least at present. The higher percentage of polyploids in high northern latitudes can be ascribed to a combination of the following causes. First, the floras of these latitudes contain an exceptionally high percentage of perennial herbs with efficient means of vegetative reproduction, or of hemicryptophytes, in the terminology of Raunkiaer. Because of their growth habit such plants are more favorably disposed toward polyploidy, as will be brought out in a later section. Second, the majority of these areas have been subjected to very drastic changes in climatic and edaphic conditions in relatively recent times, accompanying the successive advances and recessions of the Pleistocene ice sheets. Polyploids, when allopolyploid or when derived from crossing

between races or subspecies of a species, are likely to possess wide ranges of tolerance of climatic and edaphic conditions, as has been demonstrated experimentally for many interspecific and interecotypic hybrids. They are thus ideally suited to the colonization of areas newly opened to plants, and therefore floras of such areas might be expected to contain higher percentages of polyploids than those of older, more stable regions. Finally, it is likely that in some groups, particularly the grasses and the sedges, many of the polyploids may actually be more resistant to severe climatic conditions than their diploid ancestors (Flovik 1938). The evidence at present, however, indicates that this tendency is by no means general.

In an earlier publication (Stebbins 1942c) the suggestion was made that polyploids, as new genetic types, are likely to be particularly well adapted to the colonization of newly available areas, and examples illustrating this tendency were cited. These are *Iris versicolor* in the glaciated areas of eastern North America (Anderson 1936b), *Biscutella laevigata* in the glaciated portions of the central Alps (Manton 1934, 1937), *Crepis* in the portions of the northwestern United States covered by lava flows during the latter part of the Tertiary period (Babcock and Stebbins 1938), and the *Eriogonum fasciculatum* complex in the portions of coastal California subjected to elevation and faulting during the Pleistocene epoch. Others are the tetraploids of *Tradescantia* in the newly disturbed areas of the central United States (Anderson and Sax 1936, Anderson 1937b), those of *Vaccinium*, subgenus *Cyanococcus*, in the glaciated portions of eastern North America (Camp 1945), those of certain species of *Galium* in the glaciated portions of northern Europe (Fagerlind 1937), and the tetraploids of *Paeonia* in central Europe (Stern 1946, 1947). Among the 100 examples discussed in the preceding paragraph, 55 showed indications that the tetraploids had occupied newer territory than the diploids, 4 had apparently the reverse distribution, and in 41 examples no difference could be noted between the age of the areas occupied by the diploids and those of the tetraploids. In many of these, however, such evidence could probably be obtained by sufficiently careful study.

Melchers (1946) has recently proposed a scheme of genic recombination and selection in autopolyploids which would convert

them from the ill-adapted types which have resulted from nearly all experiments on the artificial production of polyploids to the highly successful polyploid species found in nature. Experimental testing of this scheme should be possible in the near future. Nevertheless, its application is limited to autopolyploids, which, according to the evidence presented in Chapter VIII, are a relatively small proportion of the successful natural polyploids.

The tendency of polyploids to occupy newly available habitats might lead one to expect a relatively high percentage of polyploidy among the weedy species which have taken over the new habitats made available by man. But Heiser and Whitaker (1947) found no significantly greater percentage of polyploidy in the weeds of California as compared to the nonweedy species. Their results are explained largely by the fact that the ruderal habitats occupied by weeds are adapted primarily to annuals, in which the percentage of polyploidy is lower than it is in perennial herbs. When the weedy annual species of two families, the Gramineae and the Compositae, were compared with the nonweedy annuals of the same families, the weeds were found to include a higher percentage of polyploids in both families, although this difference was most evident in the Gramineae.

The fact should be emphasized that polyploidy is by no means the only way in which plant species can adapt themselves to the occupation of new habitats. If at the time when they produce polyploid derivatives, diploid species still possess a wealth of ecotypes adapted to different environments, the diploids may along with the polyploids expand their distribution areas as new habitats become available. This has been true of such diploids as *Rosa blanda*, *R. woodsii*, and other roses of the section *Cinnamomea* (Erlanson 1934), of *Vaccinium angustifolium* and other diploid species of blueberries (Camp 1945), of the diploid forms of *Crepis acuminata* and *C. atribarba* ("*C. exilis*," Babcock and Stebbins 1938), of *Polygonatum pubescens* (Ownbey 1944), and of *Hieracium umbellatum* (Turesson 1922b, Bergmann 1935a). The difference in geographic distribution between diploids and polyploids can nevertheless be maintained even under these conditions, because of the tendency of the tetraploids to occupy different new habitats from those taken over by the diploids.

The present state of our knowledge concerning the effect of

polyploidy on plant distribution may therefore be summarized about as follows. Polyploids usually have different geographic distributions from their diploid ancestors, and are likely to be particularly frequent and diverse in regions newly opened to colonization by plants, except when these are suited primarily to annual species. Their areas of distribution tend to be larger than those of their diploid ancestors, but this tendency has many exceptions. In some instances they show greater tolerance of extreme environmental conditions than their diploid ancestors, but this tendency is not as marked as some authors have believed. The most valuable new information on this subject will be obtained, not from statistical studies of the frequency of diploids and polyploids in the entire flora of various regions, but from careful analysis of an increasing number of individual species groups, with attention paid both to the morphological characteristics and the interrelationships of the diploids and polyploids, as well as to their particular climatic and ecological preferences.

POLYPLOIDY AS EVIDENCE FOR FORMER DISTRIBUTIONAL PATTERNS

The tendency for some polyploids to have wider ranges of ecological tolerance than their diploid ancestors may in some instances cause them to survive after these ancestors have become extinct. As examples of such relict polyploids may be cited *Sequoia sempervirens*, the Pacific coast redwood; *Lyonothamnus floribundus*; and the living species of the genera *Fremontia*, *Psilotum*, and *Tmesipteris* (Stebbins 1940a). In other instances, the diploid ancestor or ancestors may have disappeared from the region occupied by the polyploid, but be still living in other parts of the earth. If this is the case, allopolyploids may provide valuable evidence on the past distribution of species groups and eventually of entire floras. As has already been pointed out, carefully conducted experiments of a suitable nature can make possible the identification of the actual parents of an allopolyploid or intersubspecific autopolyploid, or at least of their nearest living diploid relatives. If two diploid or low chromosome types demonstrated to be the ancestors of a particular allopolyploid are now found in regions remote from each other, one must assume that at some former period in the earth's history they had a different geographic distribution and occurred together, so that they could

hybridize to form the allopolyploid. With this information as a starting point, and with some conception of the geological history and fossil flora of the regions in which the species occur, significant inferences can often be made as to the time and place when these hybridizations took place, and therefore of the distribution of certain elements of the flora during past epochs of the earth's history.

Several examples of this nature have been given elsewhere (Stebbins 1947b,c). One of the best documented is *Iris versicolor* (Anderson 1936b). This species, the common blue flag of north-eastern North America, is a high polyploid with $2n = 108$ chromosomes, and it almost certainly originated from hybridization

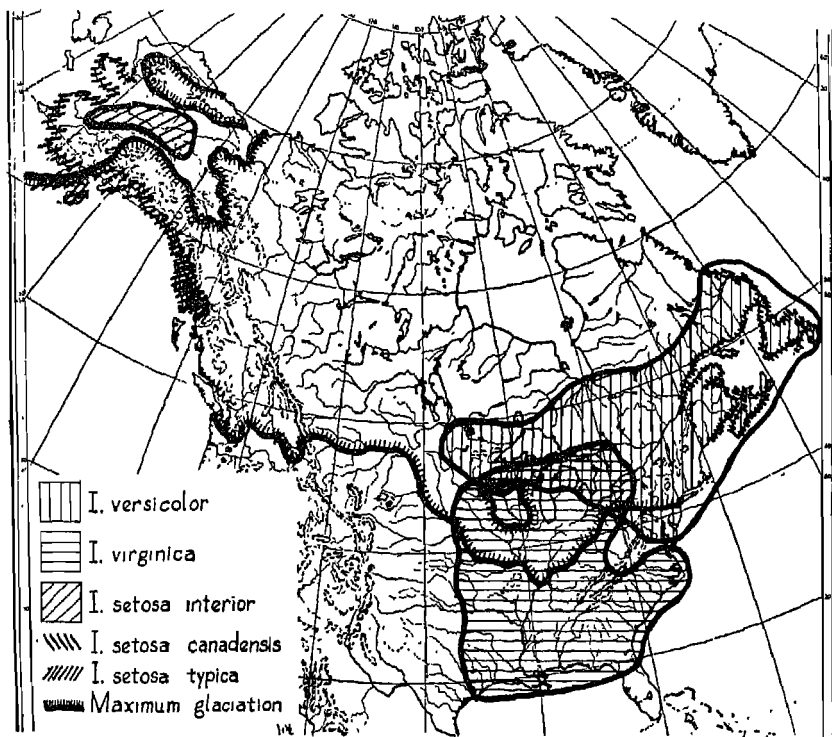


FIG. 35 Map showing the distribution of *Iris versicolor*, *I. virginica*, and *I. setosa* with its varieties *interior* and *canadensis*, and the relation of these distributions to the Pleistocene glaciation. Redrawn from Anderson 1936b. Map copyrighted by Standard Process and Engraving Co., Berkeley, Calif. Reproduced by special permission.

between *I. virginica* var. *shrevei* ($2n = 72$) and *I. setosa* var. *interior* ($2n = 36$) or some very similar form. At present, these two ancestors are separated from each other by the entire distance of 5,400 km from Minnesota to central Alaska (Fig. 35). Since *I. versicolor* occurs at present with *I. virginica*, but not with *I. setosa*, the plausible assumption is made by Anderson that at some time in the past the range of *I. setosa* var. *interior* extended south-eastward to the north central part of the United States, where it overlapped with that of *I. virginica* var. *shrevei*. There the hybridization took place which resulted in the formation of *I. versicolor*. Since the latter species is found almost entirely within the territory covered by the Wisconsin ice, it probably originated during the Pleistocene epoch. *I. setosa* var. *interior* probably occurred along the moraine of the retreating Wisconsin glaciers and was able to hybridize with the plants of *I. virginica* which advanced up the Mississippi Valley in response to the warming of the climate in late glacial times. A similar distribution of the polyploid *Oxycoccus quadripetalus* in relation to its diploid ancestors *O. microcarpus*, of northwestern North America and Eurasia, and *O. macrocarpus*, of the east central United States, led Camp (1944) to suggest a similar origin for this polyploid species. *O. quadripetalus*, however, has attained a much wider distribution than *Iris versicolor*, since it occurs in the arctic regions of both hemispheres. This may very well be due to the superior means of seed dispersal afforded by its fleshy berries.

In *Bromus carinatus* and its relatives we have a group of allopolyploids which must have originated from hybridization between diploid species of the section *Bromopsis*, now found chiefly in North America, and hexaploid species of the section *Ceratochloa*, which are at present confined to South America (Stebbins 1947b,c). Pairing of the chromosomes in appropriate hybrids indicates that if the genomic formula of the former diploids is expressed as LL, and that of the hexaploids as AABBCC, then the octoploids of the *B. carinatus* complex have the formula AABBCCLL (Stebbins and Tobgy 1944, Stebbins 1947c). Since these octoploids must have originated in North America, their hexaploid ancestors existed on this continent at some time in the past. Interpretation of the fossil grasses described by Elias (1942) from late Tertiary deposits of the North American Great Plains

suggests that the nearest living relatives of these fossils are species of the genus *Piptochaetium* now confined to South America, and indicates that other species which at present are indigenous only to temperate South America may have existed in North America in the latter part of the Tertiary period, and that the hexaploids of *Bromus*, sect. *Ceratochloa*, were among these species.

Two allopolyploids which suggest the former existence in North America of a species group now entirely Eurasian are *Oryzopsis asperifolia* and *O. racemosa*. These species have the haploid number $n = 23$ and are morphologically intermediate between North American species of the subgenus *Euoryzopsis*, having $n = 11$, and certain Eurasian representatives of the subgenus *Piptatherum*, which have $n = 12$ (Johnson 1945). The evidence summarized by Chaney (1936, 1947) on the woody plants known as fossils from the mid-Tertiary deposits of the western United States suggests that these Asiatic woodland species existed in North America during the middle or early part of the Tertiary period and that the allopolyploid species of *Oryzopsis* arose at that time.

The possibility that the New World allotetraploid species of *Gossypium* originated in North America in the early part of the Tertiary period through hybridization between one group of diploids now found only in South America and another now confined to Asia has been discussed elsewhere (Stebbins 1947b). Hutchinson and Stephens (1947) have summarized the evidence proving as conclusively as such things can be demonstrated that the New World cottons are allopolyploids of the Old World *G. arboreum* or its near relative and an American diploid closely similar to or identical with *G. raimondii*, of Peru. They have assumed that *G. arboreum* was brought from India to the New World by aboriginal man and that the hybridization and allopolyploidy which gave rise to the modern cultivated cottons took place under cultivation in South America. The difficulties of this hypothesis are discussed elsewhere (Stebbins 1947b). The possibility of the early Tertiary origin of the allotetraploid cottons is at least strong enough to warrant a search for similar examples among strictly wild species groups of the semiarid tropics.

A group of European tetraploids which gives evidence of past hybridization between diploid species groups now widely sepa-

rated from each other is that of the species of *Paeonia* related to *P. officinalis*. Evidence is given elsewhere (Stebbins 1938a, 1939, 1948) that this species and some of its relatives, particularly *P. peregrina*, arose as allopolyploids between *P. cretica*, *P. daurica*, and other southeastern European diploids on the one hand, and primarily Asiatic diploids related to *P. anomala* on the other. That these Asiatic and European species could have existed together in northern Europe during the latter part of the Tertiary period is suggested by the composition of the fossil flora of this age described by Reid and Reid (1915) from the lower Rhine basin. It contains a mixture of species still found in parts of Europe and of others now strictly Asiatic. From these examples one can see that the evidence from allopolyploidy for past distribution patterns of herbaceous plant species agrees well with that provided by fossil floras, whenever the latter are available.

FACTORS DETERMINING THE ORIGIN AND SPREAD OF POLYPLIIDY

From the evidence presented in the preceding sections certain factors can be summarized which favor the development of polyploidy in plant groups. These are of two types, internal and external. The internal factors consist chiefly of the manner of growth and the reproductive potentialities of the diploid species, as well as the genetic relationships of the existing diploid species to each other. Müntzing (1936) and the writer (1938b) have brought out the fact that polyploidy is more frequent in perennial herbs than it is in annuals. Fagerlind (1944a) and Gustafsson (1947c, 1948) have produced further data to support this conclusion, and Gustafsson has pointed out, furthermore, that among perennials those species with effective means of vegetative reproduction, such as stolons, rhizomes, bulbs, and the "winter buds" of *Potamogeton* and other aquatic plants, are more likely to be polyploid than are species without such structures. Both Müntzing and Gustafsson interpret this evidence to mean that the origin of the perennial habit, as well as of the accessory methods of vegetative reproduction, is a direct consequence of the polyploidy. But against this interpretation are the following facts. In the first place, a very large number of autotetraploids has now been produced from annual diploids belonging to a wide variety of plant genera. While some of these autotetraploids, like those of *Zea*

(Randolph 1935), have a subperennial habit, the majority of them have remained strictly annual. And there is no evidence at all that the induction of polyploidy has caused the appearance of rhizomes or any similar methods of vegetative reproduction where they did not exist in the diploid forms. On the other hand, in many of the genera showing the characteristic correlation between polyploidy and efficient vegetative reproduction, such as *Biscutella*, *Fragaria*, *Rubus*, *Antennaria*, *Arnica*, *Artemisia*, and *Hieracium*, diploid species exist in which vegetative reproduction is just as well developed as it is in the tetraploids (Fagerlind 1944a). In many instances vegetative reproduction and the perennial habit are undoubtedly intensified by the onset of polyploidy, but they are rarely if ever originated by this condition.

The undoubted correlation between frequency of polyploidy and the development of perenniality and vegetative reproduction is better explained by assuming that when such characteristics are already present in diploid species, polyploidy can arise and become established more easily than is possible in annuals or in perennials without effective means of vegetative reproduction. Such an assumption is fully warranted by the fact that in most instances the origin of polyploidy involves a period of partial sterility which may last for several generations before the polyploids have become stabilized (Fagerlind 1944a). In autopolyploids this sterility "bottleneck" is at the polyploid level. Most of the artificially induced autopolyploids are partly sterile, as was stated in Chapter VIII, and highly fertile types can be obtained from them most easily through intercrossing between autopolyploids of the same species derived from different diploid genotypes, and selection for high fertility from this heterozygous material. Fertile autopolyploids might occasionally be expected from diploid interracial hybrids, but the latter are, of course, relatively uncommon. Potential allopolyploids must face the "bottleneck" of partial sterility at the diploid level, and in the case of segmental allopolyploids this recurs in the early stages of polyploidy.

The fact that perennials with efficient means of vegetative reproduction are better equipped than annuals to pass through such "bottlenecks" is obvious and needs no further elaboration. A further significant fact is that plants with efficient means of

vegetative reproduction are better equipped to take advantage of the greater range of tolerance of extreme environmental conditions which is known to exist in many interracial and interspecific hybrids (Clausen, Keck, and Hiesey 1947). Such hybrids, if they are capable of spreading by means of stolons, rhizomes, tubers, or similar devices, may drive out their parents through direct competition, even though their ability to form viable seed is vastly inferior. Both auto- and allopolyploidy may therefore be expected most frequently in perennials with efficient means of vegetative reproduction.

Gustafsson (1948b) has also postulated that cross-fertilization, or allogamy, promotes the origin of polyploidy, while autogamy restricts it. It is certainly true that many allogamous groups have high percentages of polyploidy, while, conversely, there are many autogamous groups which lack it. It is possible, however, that this apparent correlation between allogamy and polyploidy is indirect and spurious. In Chapter V a correlation was demonstrated between allogamy and the presence of efficient means of vegetative reproduction, while a large proportion of annuals was shown to be autogamous. In order, therefore, to demonstrate a true correlation between allogamy and a high frequency of polyploidy, data should be obtained from species with the same growth habit. There is some indication that, if such data are obtained, the expected correlation will not be found. In species of Gramineae with the caespitose perennial habit, for instance, high polyploidy has been developed in many species groups of such genera as *Bromus*, *Danthonia*, and *Stipa*, which are largely autogamous through the presence of cleistogamous flowers. Also, among the annual Compositae, tribe Madinae, polyploidy is most highly developed among the autogamous species of the genus *Madia*, but is rare or lacking among the allogamous species of *Layia* and *Hemizonia*.

Clausen, Keck, and Hiesey (1945a) have suggested that certain types of interrelationships between the species of a group favor the establishment and spread of allopolyploidy. According to them, a large number of polyploids arising from interspecific hybrids with intermediate degrees of chromosome homology, that is, those characterized as segmental allopolyploids by the present writer, will be unsuccessful because of partial sterility or geno-

typic instability. That this is not entirely true is evident from the successful artificial production of such polyploids in various genera (see page 323), as well as the various natural examples cited in Chapter VIII. Nevertheless, the proportion of segmental allopolyploids which are unsuccessful is definitely higher than that of allopolyploids or amphiploids derived from widely different species. Hence, the development of allopolyploidy in a genus is greatly favored by the presence in it of many species which are sufficiently closely related to each other so that they can produce vigorous F_1 hybrids, but strongly enough differentiated so that their chromosomes are nearly or entirely incapable of pairing with each other. Conversely, the presence of many species having chromosomes partially homologous with each other restricts the ability of the group to form extensive polyploid series. Evidence from artificially produced examples indicates that autopolyploidy is rarely, if ever, successful at higher levels than tetraploidy, so that in general any one species can produce by autopolyploidy only a single other genetically distinct type.

As a rule, therefore, extensive polyploid complexes are produced only after some of the speciation processes in a genus on the diploid level have reached a certain stage of maturity, so that at least some of the species have diverged widely from the others with respect to their chromosomes. Since, as will be pointed out in Chapter XIV, rates of evolution vary widely from one group to another, this maturity may be reached in a short period of chronological time or may never arrive, depending on the group concerned. The genus *Aquilegia* is cited by Clausen, Keck, and Hiesey as one in which species differentiation has not reached the point favorable to allopolyploidy, although it belongs to one of the most primitive families of angiosperms, the Ranunculaceae, and has a distribution pattern which suggests at least a mid-Tertiary age. Whether the absence of polyploidy in *Aquilegia* can be explained on this basis is doubtful, since in genera like *Zauschneria* and *Vaccinium*, of which the species are just as poorly differentiated cytologically on the diploid level, both auto- and allopolyploidy are well developed. A better example might be the Old World species of *Crepis*, in which natural polyploids are rare, and the ones produced artificially from diploid species (*C. foetidiorubra*, *C. capillaris-tectorum*) have been unsuccessful. The only

extensive group of polyploids in *Crepis* has overcome the sterility handicap by means of apomixis, as mentioned in Chapter X. The genus *Madia* may be cited as one which is perhaps relatively young, since it consists mostly of highly specialized annuals adapted to relatively new habitats in coastal California, but which has nevertheless reached the stage of maturity in species differentiation which makes allopolyploidy successful.

The chief external factor favoring the establishment of polyploidy is the availability of new ecological niches. Unless these are at hand, the new polyploids will be forced to face competition with the already established diploids, and in such struggles they are almost certain to be at a disadvantage, particularly during the first few generations of their existence. Polyploidy, therefore, may be looked upon as a process which is most effective as a means of enabling species groups which have reached a certain stage of depletion of their biotypes, and of sharp divergence of specific entities, to adapt themselves to new environmental conditions which arise relatively suddenly. It is much less important in stable environments and in diploid species which are still widespread and rich in ecotypic differentiation.

These facts may afford the best explanation of the rarity of polyploidy among woody plants of the temperate zone (Stebbins 1938b). These plants have all of the features which various authors have considered favorable to polyploidy: long life, frequent vegetative vigor, and small chromosomes. Furthermore, the basic haploid numbers of their genera are frequently very high, such as $x = 21$ in *Platanus*, $x = 23$ in *Fraxinus* and other Oleaceae, and $x = 41$ in *Tilia*. These numbers suggest that polyploidy is possible in such genera and may have been one of the important evolutionary processes active while they were being differentiated from related genera, as discussed in the following section. The absence of well-developed polyploid series in them may indicate merely that polyploids have been at a selective disadvantage during their recent evolutionary history. Such a hypothesis is favored by the fact that many of the woody genera which are most abundant in the regions covered by the Pleistocene glaciation, such as *Salix* and *Betula*, have strongly developed polyploid series.

POLYPOIDY AND THE ORIGIN OF HIGHER CATEGORIES

Polyploidy is now widely recognized as one of the principal methods for the formation of new species among the higher plants. The species originating by this process, however, are for the most part very similar to their diploid ancestors in external morphology and in ecological preferences, or else they contain recombinations of the characteristics found in these ancestors. The long-continued evolution needed to differentiate genera, families, orders, and phyla appears to have taken place chiefly on the diploid level, or at least on the homoploid level in groups which had a polyploid origin. The evidence in favor of this assumption, which was first clearly expressed by Levitzky and Kuzmina (1927) in their study of the genus *Festuca*, by Avdulov (1931) in his cytological survey of the family Gramineae, and by Manton (1932) in her similar study of the Cruciferae, is that in most families polyploidy occurs sporadically in various genera, with the polyploids showing few if any characteristics not also found in diploid species, while the greatest scope of morphological and ecological variation, including types which form connecting links between genera, is most often at the diploid level.

Nevertheless, there is some evidence that many genera and even subfamilies or families of seed plants have had a polyploid origin. This evidence must of necessity be indirect, since these higher categories are all so old that the ancestral species which gave rise to them are almost certainly extinct, so that the polyploidy cannot be repeated experimentally, as it can in the case of many modern polyploid species. The three types of evidence which have been employed are, first, evidence from external morphology and chromosome numbers; second, evidence from "secondary pairing"; and, third, evidence from the number of satellites and nucleoli in the somatic complement.

The last two lines of evidence have been subject to frequent criticism. Secondary pairing was first clearly described and illustrated by Ishikawa (1911) and Lawrence (1931) in *Dahlia variabilis*, which is unquestionably a high polyploid with $2n = 64$ chromosomes. But its use for determining the polyploid origin of higher categories dates from the study of Darlington and Moffett (1930, Moffett 1931) on the origin of the tribe Pomoideae of the family Rosaceae. In both of these groups, the small chromosomes

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form only bivalents at meiosis, but these bivalents are arranged in groups of two or three, rather than being equally spaced on the metaphase plate. Darlington and Moffett found that in the diploid species of Pomoideae studied by them the most frequent pattern of arrangement of the 17 bivalents was in three groups of 3 bivalents and four groups of 2, and they interpreted this to mean that the tribe Pomoideae originated from diploid species with $x=7$ by doubling of the entire set, plus the addition of a third partial set consisting of 3 of the original 7 bivalents ($7+7+3=17$). The presence of $x=7$ as the basic haploid number of many genera in the family, particularly within the tribe Rosoideae, was used as supporting evidence for this hypothesis.

The concept of secondary association and interpretations based on it have been frequently criticized. Sax (1931b, 1932) found that the pattern of secondary association described by Darlington in *Pyrus* could not be recognized in other genera of the tribe, and he suggested that the Pomoideae are hypertetraploids derived from primitive Prunoidae with $x=8$ ($8+8+1=17$). Clausen (1931b), based on his studies of aneuploidy and polyploidy in *Viola*, sect. *Melanium*, expressed the need for caution in interpreting the origin of basic chromosome numbers, and he suggested that secondary association might arise as a result of segmental interchange, which could cause the occurrence of duplicated segments on otherwise nonhomologous chromosomes. Heilborn (1936) believed that secondary association is an artefact, based on a tendency for chromosomes of similar size to attract each other as they congregate on the metaphase plate. His conclusions, though they might have some validity in the species of *Carex* studied by him, which contain chromosomes differing greatly from each other in size, would be inapplicable to *Dahlia*, *Pyrus*, and other genera in which such differences do not exist. Catcheside (1937), after a careful study of secondary association in *Brassica oleracea*, including measurements and statistical analysis of the distance between the bivalents, concluded that the phenomenon is a real one, and suggested that *B. oleracea* ($n=9$) is a hyperploid derived from an ancestor with the haploid number $x=6$. Sakai (1935) and Nandi (1936) both studied secondary association in *Oryza sativa* ($n=12$), and they concluded that this

species is a hypertetraploid derived from ancestral species with $x = 5$.

One of the weaknesses of the interpretations of phylogeny based on secondary association is that most of them are at variance with conclusions reached on the basis of comparative morphological and cytological studies of the groups concerned. As between the opinion of Darlington, that the Pomoideae are derived from the Rosoideae, and that of Sax, that they are more nearly related to the Prunoideae, the latter agrees much more nearly with the morphological evidence. The Rosoideae contain a number of characteristics and tendencies not found at all or relatively uncommon in the Pomoideae: tendency toward the herbaceous or scandent habit; tendency toward yellow flowers; and carpels numerous and containing only one ovule. On the other hand, the Prunoideae more nearly resemble the Pomoideae in habit, leaf shape, inflorescence, and character of sepals and petals than does any other tribe of the family Rosaceae, and these two tribes possess in common the substance amygdalin, which is not found in the Rosoideae or in any other tribe of the family except for the two mentioned above. There are, however, certain morphological and anatomical characteristics in which most genera of the Pomoideae resemble the Spiraeoideae more than they resemble the Prunoideae, such as the presence of five carpels with several or numerous ovules (Juel 1918). On morphological grounds, therefore, the most probable inference as to the origin of the Pomoideae is that they arose as amphidiploids between primitive or ancestral members of the tribes Spiraeoideae and Prunoideae. Since the basic number most commonly found in the Spiraeoideae is $x = 9$ (Sax 1931b, 1936), while that in the Prunoideae is $x = 8$ (Darlington 1928, Sax 1931b), the basic haploid number of the Pomoideae, $x = 17$, is directly explained by this hypothesis.

The conclusion which Catcheside (1937) reached on the basis of secondary association in the genus *Brassica*, namely, that the original basic number for the genus is $x = 6$, does not agree with the conclusions reached by Manton (1932) on the basis of her comprehensive morphological and cytological survey of the family Cruciferae as a whole. She found that $x = 6$ occurs only occasionally in this family, and not at all in *Brassica* or its near relatives. Furthermore, in every instance of the occurrence of this basic

number, it is found in a species representing the specialized end point of an evolutionary series and appears to have been evolved by reduction from $x = 7$ or $x = 8$, as will be discussed in Chapter XII. Manton concluded that the most probable original basic number for *Brassica*, as for many other genera of Cruciferae, is $x = 8$.

Similarly, the conclusion of Sakai and Nandi, that the original basic chromosome number of *Oryza* is $x = 5$, is at variance with the evidence produced by Avdulov (1931) in his thorough and comprehensive survey of the family Gramineae. Avdulov showed that the basic number $x = 12$ is found not only in *Oryza* and most other genera of the tribe Oryzeae but also is by far the commonest one in the primitive genera of grasses placed by Avdulov in his series Phragmitiformes, as well as in the tribe Bambuseae. The genus *Ehrharta*, which in many respects appears more like an ancestral prototype of the Oryzeae than does any other living genus, also has $x = 12$. On the other hand, species with five pairs of chromosomes are very uncommon among the Gramineae, and this number is not found in any primitive genus, nor in any genus related to *Oryza*.

So far as this writer is aware, no critical study exists in which evidence from secondary association has been correlated with that from comparative morphology and cytology of a number of different species and genera and agreement has been found between the different lines of evidence. At present, therefore, secondary association can be considered an actual phenomenon and one which in many instances suggests the polyploid nature of a species or genus, but one which may be considerably modified by segmental interchange, duplication of chromosome segments, and other phenomena not at all related to polyploidy. It is therefore not a reliable index of the exact basic haploid number possessed by the original ancestors of a group.

Equally or more unreliable is the evidence from the number of satellites and nucleoli. The use of this evidence has been advocated most strongly by Gates, who has published a comprehensive review of the subject (Gates 1942). In some instances the possession of four satellites and nucleoli is evidence of tetraploidy, but many polyploids never have more than two of these structures. Furthermore, there are examples, such as *Leontodon incanus* and

L. asperrimus, which have only four pairs of chromosomes, two of which bear satellites, and consequently often form four nucleoli at the mitotic telophase (Bergman 1935b).

For these reasons, the only safe inferences which can be made about whether a particular basic number is of ancient polyploid origin are those based on thorough and well-correlated studies of the comparative morphology and cytology of a large number of intimately related species and genera. Even when all possible evidence has been obtained, questions such as these are open to a certain amount of doubt, and the final conclusions must be regarded as indicating which of several possible situations has the greatest degree of probability.

There is, nevertheless, evidence that polyploidy played a role in the origin of genera among the earliest of the angiosperms. Whitaker (1933) found the haploid number $x = 19$ not only in *Magnolia* and *Liriodendron*, but also in *Trochodendron*, *Tetracentron*, and *Cercidiphyllum*, woody genera of the primitive order Ranales which bear only relatively distant relationships to each other (Nast and Bailey 1945). In other woody genera of this order, namely, *Illicium*, *Schizandra*, *Kadsura*, and *Michelia*, the basic number is $x = 14$, and $x = 12$ is characteristic of one family of woody Ranales, the Lauraceae (Darlington and Janaki-Ammal 1945), while $x = 7$ is found in the genus *Anona* of another such family, the Anonaceae (Asana and Adatia 1945). Although the Magnoliaceae and their relatives obviously did not arise by allopolyploidy between any forms resembling the living Lauraceae and Anonaceae, nevertheless there exists a strong possibility that the commonest basic numbers in the primitive woody Ranales were $x = 12$ or 6, and $x = 7$. If this were true, the living Magnoliaceae and their relatives would have to be looked upon as very ancient allopolyploids which have long outlived the extinction of their diploid ancestors. The Anonaceae and the Lauraceae could be regarded as families in whose ancestors polyploidy did not become so firmly established, and which underwent much more progressive evolution on the diploid level.

Anderson (1934) has suggested that the woody Ranales and through them the angiosperms as a whole originated as allopolyploids from 12-paired ancestors related to the conifers or Ginkgoales and 7-paired ancestors related to the Gnetales. On grounds

of external morphology this suggestion is so highly improbable as to be hardly worthy of serious consideration.

Another primitive group in which polyploidy may have played an important role in the differentiation of genera is that of the subfamilies Mimosoideae and Caesalpinoideae of the Leguminosae. In both tribes, the commonest haploid numbers for several genera are $x = 12$, $x = 13$, and $x = 14$ (Senn 1938a, Darlington and Janaki-Ammal 1945). One of the largest genera of the tribe, *Cassia*, also has many, perhaps a majority of, species with these as the haploid numbers, but other species exist with $x = 8$ and $x = 7$ (Jacob 1940), suggesting that the last two are probably the basic numbers for the genus. In another genus of the Caesalpinoideae, *Cercis*, the haploid numbers found are $x = 7$ and $x = 6$. All this evidence suggests that the latter are the original basic numbers of the ancestral genera of Caesalpinoideae and Mimosoideae, and that the basic numbers found in most of the modern genera are of polyploid derivation.

In a genus of the Leguminosae, subfamily Papilionoideae, namely, *Erythrina*, the basic number almost certainly indicates an ancient polyploidy. Atchison (1947) has found either $2n = 42$ or $2n = 84$ in all of 33 species of this genus investigated. Since the commonest basic numbers found in other genera of the tribe Phaseoleae, to which *Erythrina* belongs, are $x = 11$ and $x = 10$, the basic number, $x = 21$, of this genus is probably derived by allopolyploidy. Since *Erythrina* is distributed in the tropics of both the Old and the New World, its polyploidy may be very ancient (see Chapter XIV).

Some well-known genera and subfamilies of temperate regions of which the basic number is probably of ancient polyploid derivation are *Platanus* ($x = 21$, Sax 1933), *Aesculus* ($x = 20$, Upcott 1936), *Tilia* ($x = 41$, Dermen 1932), and the Oleaceae, subfamily Oleoideae ($x = 23$, Taylor 1945). The Salicaceae probably represent such a family, since their basic haploid number is $x = 19$ (Darlington and Janaki-Ammal 1945). Many other similar examples of ancient woody genera could be cited. In an earlier publication (Stebbins 1938b), the writer pointed out that basic chromosome numbers are on the average higher in woody genera than they are in herbaceous ones, although polyploid series within genera are less frequent. At that time the suggestion was offered

that these relatively high basic numbers might have been the original ones for the angiosperms, and that the lower numbers characteristic of herbaceous genera were derived through step-wise reduction in the basic number, as is known to occur in many genera, such as *Crepis*, and will be discussed in Chapter XII. The more recent evidence, however, suggests that $x = 6, 7,$ and 8 are more likely to have been the original basic numbers for the flowering plants, and that $x = 12, 13, 14,$ and all higher basic numbers are for the most part of ancient polyploid derivation (Stebbins 1947a).

This hypothesis has important implications for the phylogeny and the evolutionary history of the flowering plants. Evidence presented earlier in this chapter indicates that polyploids are most successful as invaders of newly opened habitats. Our knowledge of the fossil floras of the Tertiary period indicates that ever since the beginning of this period the genera and families of woody angiosperms have existed in approximately their present form (see Chapter XIV). The polyploidy which accompanied their origin must therefore date from the Cretaceous period or earlier. One of the most likely hypotheses, therefore, is that the new habitats which offered themselves to the newly formed polyploids of the woody angiosperms were those made available by the decline and extinction of large numbers of gymnosperms during the early and middle part of the Cretaceous period. Once these habitats were filled, the opportunities were over for rapid bursts of evolution and the "cataclysmic" origin of species and genera among woody plants adapted to mesophytic conditions, so that after this time only isolated examples of this type of evolution occurred among such plants.

If this hypothesis is correct, students of angiosperm phylogeny should look for traces of ancient allopolyploidy resulting from hybridization between species which were the ancestral prototypes of many of our modern families. The reticulate pattern of evolution which is the typical one when allopolyploidy has occurred should characterize the interrelationships between families and orders of flowering plants. If this is actually the case, an explanation might be at hand for the fact that botanists have had much more difficulty in deciding on the true interrelationships between families and orders of flowering plants than have students of in-

sects or vertebrates when dealing with similar groupings in their organisms.

It should be emphasized, however, that this view of polyploidy as having played a major role in the origin of families and orders of flowering plants does not imply that progressive evolution is furthered by this process. In every example in which its immediate effects have been analyzable, polyploidy has appeared as a complicating force, producing innumerable variations on old themes, but not originating any major new departures. In Chapter XIII, the fact will be emphasized that the number of families of angiosperms is much larger than that of major evolutionary trends which can be traced in the group. This multiplication of families, containing various recombinations of a relatively small number of primitive and specialized morphological characteristics, may have been greatly aided by polyploidy. But neither the basic chromosome numbers of angiosperm genera nor any other type of evidence supports the concept that such progressive trends as sympetaly, epigyny, or any other of the trends in floral specialization which form the basis for the natural system of families and orders of flowering plants has been caused or promoted by polyploidy.

POLYPLOIDY IN PLANTS AND ANIMALS

One of the most interesting and puzzling features of polyploidy is the small role which it has played in animals as compared to its dominant role in the higher plants. Vandel (1938), after reviewing the chromosome numbers in the animal kingdom, reached the conclusion that polyploid species of animals are known only in hermaphroditic groups, such as pulmonate mollusks, and in parthenogenetic forms, such as rotifers, the genus *Artemia* among crustaceans, and the moth, *Solenobia*. Since the review of Vandel, three outstanding examples of actual or probable polyploidy among natural animal species have been described, namely, in the ciliate Protozoa (*Paramecium*, Chen 1940a,b), in the order Curculionidae, or weevils, among the insects (Suomalainen 1940a,b, 1945, 1947), and in the family Salmonidae among fishes (Svårdson 1945). The first two of these three examples agree with previously known ones in that the ciliate Protozoa are essentially hermaphroditic and all the polyploid Curculionidae are partheno-

genetic. But the family Salmonidae appears to represent the first example of a sexual polyploid complex, with all of its attendant difficulties of classification of species and genera, which has been detected in the higher animals.

The classic theory to explain the scarcity of polyploidy in bisexual animals, first offered by Muller (1925), is that polyploidy upsets the balance of sex determination to such an extent that regular segregation of sex factors is impossible in polyploids. This hypothesis was based on the fact that triploid individuals of *Drosophila melanogaster* are either females or intersexes, but never normal functional males. Early evidence from the plant kingdom tended to support this hypothesis. Thus, Wettstein (1927) found that polyploids produced artificially from dioecious species of mosses are monoecious or hermaphroditic, while natural polyploid species in *Bryum* and other genera are the same, a fact recently confirmed for the genus *Mnium* by Heitz (1942). Similarly, Hagerup (1927) found that the diploid *Empetrum nigrum* of Europe is dioecious, while the tetraploid *E. hermaphroditicum* of Greenland is hermaphroditic, with perfect flowers.

But the fact was realized somewhat later that typical polyploid series exist in genera of dioecious flowering plants, and that the polyploid members of these series in most cases show as regular a segregation of male and female types as do the diploids. This was pointed out for *Salix* by Müntzing (1930b), and it is also true of *Rumex acetosella* (Löve 1944), of certain polyploid but normally sexual species of *Antennaria* (Bergman 1935c, Stebbins unpublished), and of the genera *Buchloe* and *Distichlis* among the grasses (Avdulov 1931, Stebbins and Love 1941).

Direct evidence that dioecism and polyploidy are not incompatible with each other was produced almost simultaneously by Warmke and Blakeslee (1940) and by Westergaard (1940) from their studies of autotetraploid plants of *Melandrium dioicum* (*Lychnis alba* or *L. dioica*). This species has long been known to possess a typical X — Y sex-determination mechanism, with the male as the heterozygous sex. The autotetraploids of the constitution XXXX were, of course, females, but all other types (XXX \bar{Y} , XXYY, and XYYY) were entirely or essentially males, quite contrary to their counterparts in *Drosophila*. Because of this fact, the establishment of lines containing only XXXX and

XXXY types was easily accomplished, and these lines were as typically dioecious as their diploid ancestors.

These results show that the existence of functional bisexual polyploids depends on the presence in the group of a sex-determining mechanism in which the chromosome peculiar to the heterozygous sex (the Y or Z chromosome) possesses strongly dominant sex-determining factors. If these factors are only weakly dominant, or if, as postulated by Bridges for *Drosophila*, the Y or Z chromosome is neutral and the nature of the sex depends on the balance between the autosomes and the X or W chromosomes, then the sex-determining mechanism cannot work on the polyploid level. This shows that Muller's principle holds for some and perhaps the majority of bisexual animals, but could hardly be expected to be responsible for the scarcity of polyploidy in the animal kingdom as a whole.

A further reason for the scarcity of polyploidy in animals is provided by the studies of Fankhauser (1945a,b) on the morphological characteristics and the development of polyploid individuals of certain species of amphibians. In such species as *Triturus viridescens* and *Eurycea bisliniata*, eggs obtained from normal fertilization and raised artificially without special treatment regularly produce a small percentage of triploid or tetraploid individuals. Adult polyploid animals, although they can be reared in captivity, are unknown under natural conditions, and no polyploid species are known of *Triturus* or any other genus of amphibians. The artificially raised adult salamanders contain both typical males and sterile females with underdeveloped ovaries and are always weaker than normal individuals.

The causes for the weakness of artificially raised polyploid salamanders lie partly in the disturbances produced by polyploidy in the size and number of cells in various vital tissues and organs. Most of them, including the brain and the spinal cord, have fewer cells than do the corresponding organs of diploids. It is obvious that this condition would affect metabolic processes like digestion and nervous reaction. Expressed in general terms, the statement can be made that in addition to the incompatibility between polyploidy and certain types of sex-determining mechanisms, a second important barrier to the success of polyploidy in animals, as was first suggested by Wettstein (1927), is the disharmony in the

complex processes of animal development produced by this sudden alteration of the genotype. Polyploidy is successful in plants because their developmental processes are so much simpler (see Chapter V, p. 182).

The scarcity of polyploidy in animals has another important implication for students of this phenomenon in plants. Long-continued trends of specialization and the production through adaptive radiation of families and orders adapted to particular modes of life have been much more characteristic of evolution in animals than in plants. The fact itself is additional evidence in favor of the conclusion expressed in the previous section of this chapter, namely, that polyploidy, although it multiplies greatly the number of species and sometimes of genera present on the earth, retards rather than promotes progressive evolution.

THE PRACTICAL SIGNIFICANCE OF POLYPLOIDY

The practical value to plant breeders of an intimate knowledge of the natural processes of evolution has been previously emphasized earlier in this book, particularly in connection with ecotype differentiation and interspecific hybridization. Polyploidy is not only one of the best known of evolutionary processes; in addition, it is the most rapid method known of producing radically different but nevertheless vigorous and well-adapted genotypes. For these reasons, it is the large-scale evolutionary process most suitable for development as a technique in plant breeding.

Nevertheless, attempts to use polyploidy as a plant breeding technique have up to the present not proved entirely successful. This is partly due to the fact that methods of producing polyploids in large quantities have been known for only twelve years, six of which were disturbed by a great war and the inevitable retardation of agricultural research which it caused. But in addition, evidence obtained from the large-scale production of artificial polyploids has shown that many conceptions previously held about polyploidy are only partly true. Before artificial polyploidy can be used by plant breeders with the greatest possible efficiency, both its particular advantages and its limitations must be thoroughly understood. Finally, the nature of artificial polyploids has demonstrated the fact that, although polyploidy is not necessarily a slower technique than the older method of intervarietal

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hybridization and selection, it is also no more rapid. Newly produced artificial polyploids are rarely if ever of economic value; they must be adapted to the needs of the breeder by means of selection and testing just as do newly produced hybrids. In view of this fact, and of the fact that the production and introduction to agriculture of a new variety of such a crop as wheat requires about fifteen years, it is not surprising that as yet no new variety of crop plant produced through artificial polyploidy has found its way into large-scale agriculture.

The use of polyploidy as a tool in plant breeding was not possible until a satisfactory method was obtained for producing polyploids on a large scale. This was achieved by the colchicine technique, as mentioned in Chapter VIII (p. 299). Other chemical substances have also been found to double the chromosome number of plants, but, as shown in the careful experimental comparison by Levan and Ostergren (1943), none of them is as efficient as colchicine.

The numerous polyploids produced with the aid of colchicine include both autopolyploids and allopolyploids of various types. As mentioned in the preceding chapter, the effects of induced autopolyploidy are various, but in some instances the polyploids, when first produced, have possessed economically desirable qualities. In ornamental flowering plants, these qualities have been a greater durability and a heavier texture (Emsweller and Ruttle 1941), while in crop plants they have consisted largely of higher concentrations of valuable substances such as vitamins and various types of proteins, of increased size of seeds, and in some forage crops, such as red clover (*Trifolium pratense*), of a greater yield of dry matter (Randolph 1941, Levan 1942b, 1945, Noggle 1946). These have, however, been balanced in most instances by various undesirable qualities, chiefly slower growth and lower fertility. The reduced seed fertility is the chief drawback of autopolyploids of cereal crops and others in which the fruits are chiefly used. The only such crop in which autopolyploidy appears to have effected an immediate improvement is buckwheat (*Fagopyrum esculentum*, Sacharov, Frolova, and Mansurova 1944).

As mentioned in the preceding chapter, the reduced fertility of autopolyploids is nearly always greater when their diploid progenitors are homozygous. For this reason, successful autopoly-

ploids can never be expected from pure lines of self-pollinated diploids. The best possibility for obtaining desirable autopolyploid varieties of such plants lies in the production of polyploids from many different diploid lines with various desirable characteristics, with subsequent hybridization and selection from this initially diverse material. In fact, Levan (1945) has pointed out that since polyploidy radically affects the balance of multiple factors acting on a single character, this proper balance, even in the case of allogamous plants, must be restored by hybridization and selection from a wide range of genetic material at the tetraploid level.

As Wettstein (1927), Levan (1942b), and many other workers have found, the chromosome numbers of a species can under no conditions be doubled indefinitely without deleterious results. Although some autotetraploids are equal to or superior to their diploid progenitors in vigor or other desirable qualities, autooctoploids are nearly always so abnormal as to be sublethal, although this effect is much more pronounced in some plants than it is in others. For each species, there is an optimum chromosome number, which may be diploid, tetraploid, or hexaploid, but is rarely higher. As yet no way is known of predicting from the characteristics of a diploid what its optimum degree of ploidy may be. The writer's experience in the genus *Bromus* (Stebbins 1949b), as well as the series of chromosome numbers known in such genera as *Buddleia*, which reaches $2n = 300$ (Moore 1947), and *Kalanchoe* (Baldwin 1938), which reaches about 500, indicate that these limits are much more flexible in allopolyploids.

If we judge by the frequency with which the different types of polyploidy appear among crop plants, we must consider allopolyploidy to be more important to agriculture than autopolyploidy. Six of the major crop plants may be autopolyploid species, but available evidence for most of these indicates that they are just as likely segmental allopolyploids, and some of them may be typical allopolyploids. These are the potato (*Solanum tuberosum*, Lamm 1945), coffee (*Coffea arabica*, Krug and Mendes 1941), banana (*Musa* vars., Cheeseman and Larter 1935, Wilson 1946, Dodds and Simmonds 1948), alfalfa (*Medicago sativa*, Ledingham 1940), peanut (*Arachis hypogaea*, Husted 1936), and sweet potato (*Ipomoea batatas*, King and Bamford 1937). On the other hand,

there are five leading crops and several minor ones in whose ancestry allopolyploidy has certainly played a major role. The origins of tobacco and cotton have been discussed earlier in this book. The other leading crop plants which are allopolyploids or partly of allopolyploid derivation are wheat, oats, and sugar cane (Bremer 1928, Grassl 1946), while less important allopolyploid crop plants are plums, apples, pears, loganberries and other commercial berries of the genus *Rubus*, and strawberries.

The commercial wheats form one of the most striking examples of allopolyploidy in the plant kingdom, and they show what may be expected from this process in the future development of crop plants. The tetraploid wheats of the emmer or *durum-dicoccum* series were apparently derived from the wild tetraploid species *Triticum dicoccoides* of Syria (Aaronsohn 1910). The formula given these wheats by Kihara (1924) is AABB, suggesting an allopolyploid origin, a theory supported by the fact that they regularly form 14 bivalents at meiosis. The A and B genomes are, however, closely related genetically, and under some circumstances chromosomes belonging to these two genomes may pair with each other. The ancestral *T. dicoccoides*, therefore, may have originally been a segmental allopolyploid which became diploidized in response to natural selection for high fertility. The hexaploid wheats, which comprise the typical bread wheats (*T. aestivum* or "*T. vulgare*"), contain the A and B genomes, although in some varieties these are considerably modified, as is evident from irregularities in pairing in hybrids between certain hexaploid wheats and the tetraploids (Love 1941). In addition they have a third genome, C, the chromosomes of which are nearly or entirely incapable of pairing with those belonging to A and B.

The identification of this C genome is one of the most interesting chapters in the history of polyploidy and reveals the occurrence in prehistoric times of one of the greatest miracles in agriculture. The hypothesis that this genome is derived, not from *Triticum* in the strictest sense, but from the related genus or subgenus *Aegilops* has been suggested by many authors. With the arrival of the colchicine technique, Thompson, Britten, and Harding (1943) were able to produce an allopolyploid from the hybrid between *Triticum dicoccoides* and *Aegilops speltoides*. This artificial allopolyploid for the most part had 21 pairs of chro-

mosomes at meiosis, was reasonably fertile, and its hybrids with forms of *Triticum aestivum* were partly fertile, although they had rather irregular meiosis. Later, McFadden and Sears (1946) produced a somewhat similar allopolyploid, using as parents *T. dicoccoides* and *A. squarrosa*. This proved to be highly fertile, and in external morphology it closely resembled the *Triticum spelta* form of *T. aestivum*. F₁ hybrids between the artificial allopolyploid and *T. spelta* formed 21 bivalents at meiosis and were fully fertile, showing that this newly created allopolyploid, *T. dicoccoides-A. squarrosa*, had essentially the chromosomal constitution of the bread wheats. There is little doubt, therefore, that the typical bread wheats (*Triticum aestivum*) originated from hybrids between the emmer or hard wheats and the weedy grass *Aegilops squarrosa*.

A. squarrosa is a small, useless weed with hard glumes or husks, long divergent awns, or beards, and a fragile, shattering inflorescence, which grows in abundance on the borders of wheat fields in many parts of the Near East, from the Balkans to Armenia, Iran, and Afghanistan. The original hybridization and doubling probably took place in southwestern Asia, between cultivated emmer-type wheat and plants of *A. squarrosa* infesting its fields (McFadden and Sears 1946).

The origin of the *vulgare* type wheats illustrates two points about natural allopolyploidy which are of the greatest importance to plant breeders. In the first place, the diploid parents of agriculturally valuable allopolyploids need not themselves possess outstanding qualities. As in the case of inbred lines of maize, and perhaps to an even greater extent, it is the combining ability that counts. Secondly, the origin of successful natural allopolyploids involves a succession of rare accidents. Therefore, given human purpose, a thorough knowledge of the new qualities desired and of the genetic make-up and interrelationships of the diploid species available, and a not inconsiderable amount of patience and perseverance, plant breeders should be able to create allopolyploids better suited to the needs of mankind than any which nature has produced, and to do this in a vastly shorter period of time.

Any program of breeding for improved new allopolyploid types must include not only a careful study of the interrelationships

of the species concerned and of the most suitable methods for hybridization and doubling the chromosome number but, in addition, a full realization of the limitations of this method. As has been emphasized in Chapter VIII, a large proportion of vigorous interspecific hybrids yield unsuccessful allopolyploids, partly because of irregular chromosome pairing at the polyploid level and partly because of the presence of some other type of sterility. As yet, no generalizations can be made by which the success or failure of an allopolyploid can be predicted with any degree of certainty, even after the F_1 diploid hybrid ancestral to it has been obtained, but some guiding suggestions can be made, based on the experience of various workers in this field.

In the first place, the increase in fertility of a doubled hybrid is due principally to one cause, namely, a change in the manner of pairing of the chromosomes due to the presence in the allopolyploid of two completely homologous sets. If the sterility of the diploid hybrid is due to some cause other than the lack of similarity between the chromosomes, the allopolyploid will be no more fertile than its undoubled progenitor. F_1 hybrids with abortive flowers, with anthers that fail to produce normal arche-sporial tissue and microspore mother cells, or with carpels that do not form normal ovules cannot be expected to yield successful allopolyploids. As mentioned in the preceding chapter, there are various additional types of sterility, which become evident only after the chromosome number of the hybrid has been doubled. In some instances of genic sterility, as in the fertile *Nicotiana sylvestris-tomentosiformis* line produced by Kostoff (1938a, Greenleaf 1941), this type of sterility can be circumvented. But in general, the breeder must expect that a considerable proportion of the allopolyploids he produces will be unsuccessful because of sterility factors which cannot be eliminated.

One type of sterility which can be controlled in at least some instances is that found in the allopolyploid between wheat and rye (*Triticale*, or *Triticum aestivum-Secale cereale*). Strains of this allopolyploid have now been in existence for over fifty years, and although many show desirable qualities of luxuriance, hardness, and large size of grain, none has as yet become sufficiently fertile and productive to succeed as a commercial crop. Müntzing (1939), after an analysis of four different strains of *Triticale* and

of various hybrids between them, concluded that the original cause of this sterility, as well as of the fact that some strains of this allopolyploid segregate weak individuals, lies in the fact that rye is normally a self-incompatible, cross-pollinated plant. Normal rye plants are all or nearly all heterozygous for lethal or semilethal genes, so that when artificially inbred they yield a large majority of weak and partly sterile individuals. The allopolyploid strains which have originated from wheat \times rye hybrids by the functioning of unreduced gametes, as is true of most of the strains now available, also contain rye genomes heterozygous for lethal and semilethal genes, which are forcibly inbred because of the dominance of factors for self-fertility present in the wheat genomes. The segregation of weak and sterile types is therefore to be expected. Müntzing (oral communication) has suggested that this difficulty may be overcome by using as the original parent a strain of rye rendered relatively homozygous and vigorous by inbreeding and rigid selection over several generations. The same difficulties and considerations will apply in every example of an allopolyploid which combines the genomes of a self-compatible and a self-incompatible species. Among these may be mentioned the perennial wheats produced from hybrids between *Triticum* and *Agropyron*. It is possible that better success with these allopolyploids may be obtained by first breeding the *Agropyron* parent for constancy, vigor, and fertility.

Since much of the sterility in allopolyploids results from the formation of multivalents and other types of abnormal pairing, reduction in fertility can be expected if the diploid hybrid which gives rise to the allopolyploid has any amount of chromosome pairing, although, as stated in Chapter VIII, there is no correlation between the amount of pairing in the F_1 hybrid and the degree of sterility found in its derivative allopolyploid. Furthermore, the sterility originating from this cause may in many instances be overcome by selection in later generations, although this is not always true. At present, the cytogeneticist does not yet have enough knowledge of the causes of sterility to enable him to make more than the tentative suggestions given above for the guidance of plant breeders. More information on the nature of hybrid sterility is badly needed.

Allopolyploids or amphiploids can be used in plant breeding in

three different ways. The first is the relatively modest aim of transferring across a barrier of interspecific sterility a valuable character which is carried by a single genetic factor. An outstanding example is the transfer of the necrotic lesion type of resistance to the tobacco mosaic disease from *Nicotiana glutinosa* to *N. tabacum* by means of the amphiploid *N. digluta* (Holmes 1938, Gerstel 1943, 1945a). In this instance, backcrossing of *N. digluta* to *N. tabacum*, followed by selfing, produced plants with the entire chromosomal complement of *N. tabacum* except for the single chromosome bearing the desired factor. The success of this method depends not only on the fertility of the amphiploid but, in addition, on the viability and the fertility of the alien substitution race (Gerstel 1945a), which contains a whole chromosome pair foreign to the species of crop plant in which it resides. It is likely that the method will be successful in economic species which are themselves polyploid, but not usually in diploid crop plants.

The second use of amphiploids is the incorporation into a valuable crop plant of some desirable characteristic which is controlled by many genetic factors. Perhaps the most outstanding example of this is the use of the amphiploids between wheat and various species of *Agropyron* to produce perennial wheat. The extensive literature on this subject cannot be reviewed here; the reader may be referred to the papers by Peto (1936), White (1940), Love and Suneson (1945), and Sule (1946). Amphiploids between *Triticum* and *Agropyron* have been produced independently in Russia, Canada, and the United States. The earliest, those of the Russian worker Tsitsin, have yielded more favorable combinations of perenniality, high productivity, and desirable grain quality than have the Canadian and the American amphiploids. Unfortunately, they have not been subjected to careful cytological studies by modern methods, so that their chromosomal constitution is almost unknown. Sule (1946) has suggested that winter wheats, which already possess winter hardiness of the vegetative parts, are the most suitable wheat parents of such amphiploids, and he has indicated that the best method of improvement is through the intercrossing of different amphiploids, as well as of strains derived from backcrossing to wheat. The degree of stability and constancy of these Russian amphiploid derivatives has not been carefully

described in publications, and the degree of regularity of their chromosome behavior is not known. But Love and Suneson (1945) found a high degree of chromosomal irregularity and inconstancy in fertile derivatives from amphiploids involving *Triticum durum*, as well as *T. macha* and *Agropyron trichophorum*. They have not been able to obtain constant, highly fertile, and productive strains which combine perenniality and the desirable grain quality of the bread wheats. The difficulty of obtaining such types lies partly in the complex genetical basis of the perennial condition, but perhaps more important is the irregular chromosome behavior in backcross types from the original amphiploid to wheat. Since none of the initial amphiploids containing the complete chromosome set of *Agropyron* in addition to that of wheat have the required quality of grain, backcrossing is necessary in order to produce useful perennial wheats. Although perhaps not impossible, the goal of producing a constant perennial wheat with productivity and quality equal to that of the best of the present annual varieties has not been reached and will require a large amount of time, patience, and skill on the part of plant breeders.

McFadden and Sears (1947) have suggested that in wheat the transfer of desirable genes from one polyploid species to another can be most efficiently carried out by the use of entire genomes; a procedure which they term "radical wheat breeding." For instance, if the breeder wishes to transfer genes for disease resistance from the tetraploid *Triticum timopheevi* to the hexaploid *T. aestivum*, he should not do this via direct hybridization between the two species, but should first obtain an allohexaploid between *T. timopheevi* and *Aegilops squarrosa*, since the latter species contains the C genome which is present in *Triticum aestivum*, but absent from *T. timopheevi*. This synthetic allohexaploid would hybridize more easily with *T. aestivum* than would *T. timopheevi*, and the F₁ would have a more regular meiosis and would be more fertile. Backcrossing this F₁ to a desirable variety of *T. aestivum* should permit the incorporation into this variety of any genes or chromosome segments from *T. timopheevi* that might be needed. Theoretically, this method should be more efficient than direct hybridization. Nevertheless, since hybridization and allopolyploidy often lead to quite unexpected results, the method should be tried out on a relatively large scale before being recommended without qualification.

The third use of amphiploids is as entirely new crop plants with qualities different from any now known. These are not likely to be useful in such crops as cereal grains, cotton, and tobacco, in which standards of quality have been established and stabilized for a very long time and must be met by any new variety which is to be useful to the processors of these crops. On the other hand, in the newer types of crop plants, particularly in plants used for animal feed and for forage, in which vigor, productiveness, and adaptability to various environmental conditions are the chief desirable qualities, there is room for many new amphiploid types.

Among the newer crops which have risen by amphiploidy in recent years, perhaps the most notable are the various berries related to the blackberry and the raspberry, of the genus *Rubus*. A careful account of these, containing a good review of the literature, is given by Clausen, Keck, and Hiesey (1945a). Two typical examples are the nessberry, an allotetraploid derived from the diploid species *R. trivialis* and *R. strigosus*, and the loganberry. The latter is apparently a typical allopolyploid, although its origin was of an unusual nature. Thomas (1940b) has shown that it must have originated from a hybrid between the Pacific coast dewberry, *R. ursinus*, and the cultivated raspberry, *R. idaeus*, and that a diploid pollen grain of the latter species must have functioned to produce it. Since *R. ursinus* is an autoallopolyploid, with the genomic formula AAAABBBBB, and *R. idaeus* may be given the formula II, the F₁ hybrid of the type described above had the formula AABBI and was therefore at once constant and fertile.

The use of allopolyploids as improved types of forage plants is just beginning. Armstrong (1945) has suggested that the *Agropyron-Triticum* allopolyploids will be more useful in Canada as forage plants than as perennial grains. Clausen, Keck, and Hiesey (1945b, and unpublished) have found that amphiploid apomicts produced by hybridizing widely different species of *Poa* have unusual vigor and adaptability to a wide range of ecological conditions. Similar characteristics have been found by the writer (Stebbins 1949b) in various amphiploids in the genus *Bromus* and in the tribe Hordeae. The habitats for which these new types of forage plants are designed are on theoretical grounds ideally

suiting to colonization by newly formed amphiploids. They are in some respects, particularly the climate and the underlying soil formation, essentially similar to habitats which existed before the arrival of man. But man's activity in clearing trees and brush, in introducing large numbers of grazing animals, and in allowing the natural cover to become greatly depleted, has so altered the original conditions that the plants constituting the original vegetation are unable to grow as vigorously and abundantly as they formerly did, even under the most careful system of management of the land. The restoration of the world's depleted range and pasture lands can be accomplished to a great extent by proper management and by reseeded with old species known to be adapted to the area concerned. But the progressive plant breeder, if he can produce plants particularly adapted to the new conditions which will prevail on such restored and well-managed lands, should be able to increase greatly their productivity, and so make more worth while the effort and expense required for proper management practices. Amphiploids, because they involve the potential achievement in a short time of an entirely new range of adaptability, should be the ideal type of plant on which to base such a program of breeding. Furthermore, controlled experiments, designed to follow the adaptation of these newly created amphiploids to their new habitats, should enable evolutionists to observe selection in action under almost natural conditions. The use of amphiploids for revegetation of depleted grazing lands, therefore, should provide a medium by which a program of agricultural improvement can be combined with fundamental experimental studies on the dynamics of evolution.