

for this purpose is about the effects of polyploidy when induced artificially in genetically balanced individuals belonging to a good species.

Morphological and physiological effects of polyploidy

These effects have long been known and are well described in a number of publications.²⁰⁹ The most immediate and universal effect is an increase in cell size (Fig. 5.1). This does not always increase the size of the plant as a

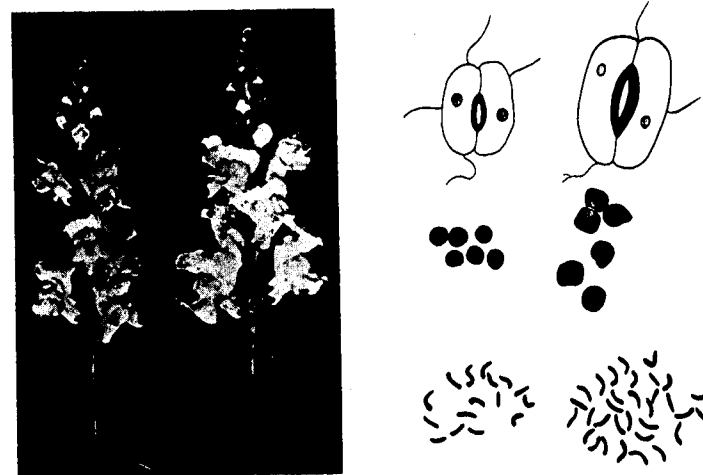


Fig. 5.1 Inflorescences, stomata, pollen and chromosomes of diploid (left) and tetraploid (right) snapdragon (*Antirrhinum majus*). (From Bamford and Winkler.¹²)

The Morphological, Physiological, and Cytogenetic Significance of Polyploidy

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INTRODUCTION

The most wide-spread and distinctive cytogenetic process which has affected the evolution of higher plants has been polyploidy, the multiplication of entire chromosomal complements. Between 30 and 35 per cent of species of flowering plants, and a considerably higher percentage of ferns, possess gametic chromosome numbers which are multiples of the basic diploid number found in their genus. This fact, however, by no means indicates the amount of polyploidy which has taken place during the entire evolutionary history of vascular plants. As pointed out in the next chapter there is now good evidence to suggest that all genera or families having basic numbers of $x = 12$ or higher have been derived originally by polyploidy from groups having lower numbers, and that even the numbers $x = 10$ and $x = 11$ may often be of polyploid derivation. If this is true, then all of the modern species belonging to many prominent families, such as Magnoliaceae, Winteraceae, Lauraceae, Monimiaceae, Fagaceae, Juglandaceae, Salicaceae, Meliaceae, Ericaceae, and Oleaceae, are derivatives of evolutionary lines which at some time in their history have undergone polyploidy.

Why has polyploidy been of such overriding importance in the evolution of higher plants? The information presented in this chapter is designed to provide an answer to this question. The first kind of information needed

whole, or even its individual organs, since a common effect of polyploidy is a reduction in the number of cell divisions which take place during development. The *gigas* effects of polyploidy are, however, commonly found, particularly in organs having a highly determinate pattern of growth, such as flowers and seeds. The increase in cell size may be reflected in larger vacuoles, and hence a higher water content of the plant as a whole, with a consequent reduction in its degree of resistance to drought and cold. This effect is, however, by no means universal.

In many instances, though not always, polyploidy causes changes in shape and texture of organs. The leaves and petals of polyploids are usually thicker and firmer than those of their diploid progenitors. Leaves and other organs are usually shorter and broader. The amount of branching is usually reduced, particularly that of tillering in polyploid grasses. The retardation of the mitotic cycle often brings about later flowering and fruiting in polyploids as compared to their diploid ancestors.

One important effect of polyploidy is a lowering of fertility and seed production. This comes about in a number of ways. In the first place, the meiosis of artificial autopolyploids is disturbed. Instead of forming exclusively bivalents, they usually form a variable percentage of quadrivalents, trivalents, and univalents. This may lead to irregularities of chromosomal segregation, and the consequent formation of gametes with unbalanced chromosome numbers. In addition, autopolyploids may be partially sterile because of various kinds of physiological unbalance, in spite of nearly regular meiotic behaviour and chromosomal segregation.

The adaptive inferiority of raw autopolyploids and ways in which it can be overcome

The characteristics just summarized by which raw, newly formed autopolyploids differ from their diploid progenitors nearly all contribute to their adaptive inferiority. It is not surprising, therefore, that such autopolyploids, which have been produced artificially in a large number of genera, have nearly always proved to be inferior to the diploid genotypes from which they arose. This inferiority is expressed in lower production of biomass per unit time, in lower seed production, and often in lowered ability to complete with diploids in artificially controlled experiments.⁶⁸ In experiments designed to test the relative success of artificially produced autotetraploids as compared to their diploid progenitors under more or less natural conditions,²¹⁰ the tetraploids have in nearly every experiment proved to be inferior. Artificially produced octoploids derived by a second doubling from experimental autotetraploids are usually sublethal.^{90,133} Clearly, chromosome doubling by itself is not a help but a hindrance to the evolutionary success of higher plants.

We must assume, therefore, that in nature successful polyploidy has been accompanied by other genetic-evolutionary processes which have compensated for the initial adaptive disadvantages of raw autopolyploids. Two kinds of processes can be postulated: gradual modification of genotypes through mutation, genetic recombination and selection; and their mass modification through hybridization, either preceding or following the chromosome doubling, followed always by natural selection for adaptive segregates. Since natural selection is equally important in connection with both processes, our task is to estimate which of the two processes has been the more important: individual mutation and genetic recombination; or hybridization and the extensive genetic recombination to which it gives rise in later generations, along with stabilization of adaptive hybrid derivatives. We can make this estimate in two ways. First, we can deduce on theoretical grounds which process might be expected to be the more effective, and second, we can analyse examples of polyploidy in nature,

and can make reasonable conclusions as to which processes have figured the most prominently in their evolution.

Disomic v. tetrasomic inheritance

From the theoretical point of view, the most important fact is that chromosome doubling changes the nature of genetic segregation from the disomic to the tetrasomic pattern. As pointed out in Chapter 1, tetrasomic inheritance decreases greatly the frequency of genotypes homozygous at a particular gene locus, and hence of those which would exhibit a characteristic controlled by a recessive allele. If the gene locus is so close to the centromere that complete linkage occurs, the F_2 phenotypic ratio for a recessive phenotype is converted from 3 : 1 (disomic) to 35 : 1 (tetrasomic). If the gene locus is so far away from the centromere that crossing over occurs regularly between them, then the F_2 ratio is 21 : 1. In any case, polyploidy greatly reduces the chance of establishment of recessive mutations. Dominant mutations are, of course, affected differently and their spread may actually be promoted by autopolyploidy.

Perhaps more important in a consideration of evolutionary processes is the effect of polyploidy on mutations which individually have small effects, and which collectively give rise to character differences that are governed by multiple factor inheritance. This importance is due to the fact that differences between natural populations with respect to adaptive characteristics are under multiple gene control. A theoretical example of what is likely to happen is presented in Figure 5.2. This figure shows the distribution of variants with respect to a quantitative character in the F_2 progeny of a cross between two parental individuals which differ with respect to genes at seven different loci. The alleles at these loci are assumed to segregate independently, to have additive effects on the character, and to be neither dominant nor recessive. If inheritance is disomic, as in a diploid, the curve of distribution is the broader, lower one expressed by the solid line. Tetrasomic inheritance, with chromosome or centromere segregation, gives the narrower, more peaked curve. This diagram shows that in crosses between races that differ with respect to quantitative characters, chromosome doubling in the progeny tends to buffer intermediate genotypes and reduce the effects of genetic segregation. Such genotypes often possess hybrid vigour. Hence this desirable characteristic may also be buffered by tetrasomic inheritance.

On the basis of these deductions, we can conclude that chromosome doubling will most often have a retarding effect on evolutionary change via mutation, genetic recombination, and selection. If this is so, we would not expect these latter processes by themselves to be very effective in counteracting the deleterious initial effects of chromosome doubling

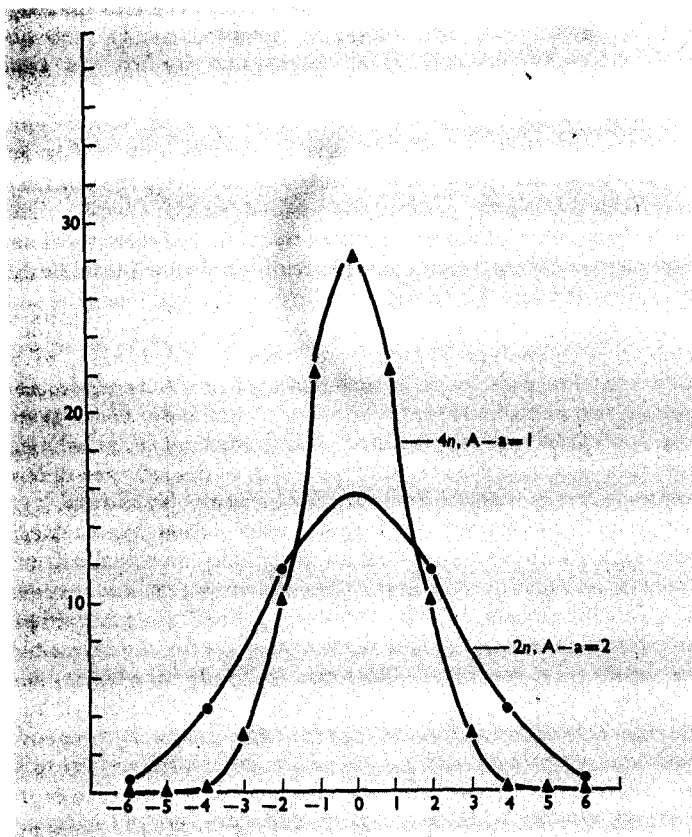


Fig. 5.2 Diagram showing the reduction in variation which would be expected in an F_2 progeny segregating for a quantitative character at the tetraploid level as compared to the diploid level. Further explanation in the text. (From Stebbins.²¹⁰)

on a balanced genotype. On the other hand, the conservatism of segregation in progeny of these doubled genotypes could be overcome by introducing through hybridization large numbers of different genes with varied effects, thus increasing the amount of genetic segregation, and enlarging the gene pool upon which selection can act.

INTERNAL FACTORS PROMOTING POLYPLOIDY

Two kinds of internal factors strongly affect the frequency of polyploidy within a group: growth habit and breeding system. In respect to growth

habit, the higher percentages of polyploidy within a modern genus are found in perennial herbs, and the lowest in annuals. The figures for woody plants are intermediate, but approach more nearly those for annual than for perennial herbs (Table 5.1).

Table 5.1 Frequency of polyploidy in genera having different growth habits, in temperate and tropical regions. The table includes only genera of which ten or more species are reported, and which are homogeneous as to growth habit. Polyploids are scored on the basis of having multiples of the lowest number recorded for the genus, regardless of the relationship of this number to that of other genera in the family.

Growth habit and distribution	No. genera recorded	Per cent of genera having:			
		0-25% polyploids	26-50% polyploids	51-75% polyploids	> 75% polyploids
Woody temperate	52	60	27	11	2
Woody tropical	13	84	8	8	0
Perennial herbs temperate	145	28	37	20	15
Perennial herbs tropical	55	61	13	13	13
Annuals temperate	21	57	24	19	0

Within the category of perennial herbs there is, moreover, a correlation between efficient vegetative reproduction, particularly by rhizomes or stolons, and high percentages of polyploidy. This correlation is particularly evident in the Gramineae. In the tribe Hordeae, for example, the genus *Hordeum*, which consists entirely of caespitose bunch grasses, contains several diploid perennial species. On the other hand in the genera *Agropyron* and *Elymus*, which contain both caespitose and rhizomatous species, all of the known diploids are either caespitose or annual. All of the rhizomatous species have tetraploid, hexaploid or higher chromosome numbers. The same situation prevails in *Bromus*, *Festuca*, *Agrostis*, *Calamagrostis*, *Spartina*, *Phragmites*, *Panicum*, and other genera. In the Liliaceae, many of the strongly rhizomatous genera (*Smilacina*, *Clintonia*, *Maianthemum*, *Convallaria*) have basic numbers of $n=16$ or $n=18$, indicating a secondary polyploid origin.

These facts support the general hypothesis maintained in this discussion, that polyploids in their initial stages depend upon especially favourable combinations of circumstances for their survival and perpetuation, but that once they have become successful are more competitive and aggressive than related diploids. Most raw polyploids, particularly those having irregular meiosis must pass through a 'bottleneck' of semi-sterility. They are much better equipped to do this if they are long-lived perennials

than if they are annuals, and are even more so if they can spread vegetatively by means of rhizomes or stolons. Moreover, as compared to caespitose or annual species, rhizomatous species are much more likely to crowd each other out if they adapted to similar habitats. Hence a highly successful rhizomatous polyploid has a particularly good chance of eliminating its diploid ancestor by direct competition or interaction, and thus making it extinct.

The low percentage of polyploids among most modern genera of woody plants can probably be explained by entirely different factors, which are primarily ecological and historical. This problem is discussed in the next chapter (pp. 194-196).

The most significant factor of the genetic system in relation to the frequency of polyploidy is the amount of outcrossing as compared to self fertilization. In woody plants, at least those of the temperate zone, this factor is of little consequence, since most of them are predominantly or exclusively outcrossing. In perennial herbs polyploidy appears to be just as common in self fertilizing as in outcrossing species. In annuals, however, the situation is different. Polyploidy in annual flowering plants is almost entirely confined to groups which have a high proportion of self fertilization in both the polyploids and their diploid ancestors.

This situation is most clearly evident in certain genera containing some annual species that are predominantly outcrossing and others that are largely self fertilizing. In them, the outcrossers are exclusively diploid, but the selfers may include a smaller or larger proportion of polyploids. Examples are *Eschscholzia*, *Mentzelia*, *Clarkia*, *Gilia*, *Amsinckia*, *Plantago*, and *Madia*. At first glance, one might conclude from this correlation that, in annual groups, polyploids are not likely to be of hybrid origin. This, however, is not the case. A hybrid origin has been demonstrated for annual polyploids in *Clarkia*,¹³⁹ *Gilia*,⁸⁵ *Amsinckia*¹⁸³ and *Madia*,²⁰⁹ as well as for polyploids in grass genera such as *Aegilops*,¹²³ which do not contain any perennials or outcrossing diploids.

Consequently, the correlation between polyploidy and self fertilization among annual species is best explained as an extension of the 'bottleneck' hypothesis. If polyploidy arises in a single individual, the chances that it can produce progeny through crossing with another individual are very low, because of the hybrid incompatibility between plants having different chromosome numbers. If the plant is perennial, and particularly if it is equipped with a highly efficient mechanism for asexual reproduction, this low probability can be realized often enough so that given hundreds or thousands of years and the successive appearance of many isolated polyploid individuals, polyploids will eventually become established and successful. If, on the other hand, the initial polyploid individual is a short-lived annual, its only possibility of ever giving rise to a successful and established

species lies in its capability for self fertilization, so that crossing is not required for its perpetuation.

RELATIONSHIPS BETWEEN POLYPLOIDY AND HYBRIDIZATION

These theoretical deductions lead us at once to the question: to what extent has hybridization accompanied polyploidy in the evolution of higher plants? Before we attempt to answer this question, we must be very clear in our minds as to what we mean by hybridization.

In cytological literature, the relationship between hybridization and polyploidy has often been obscured by the attempt to divide polyploids into two sharply defined categories, autopolyploids and allopolyploids. When first made by H. Kihara and his associates, this distinction was very useful in showing that when combined with wide crossing, chromosome doubling has very different effects from those which it has on balanced, non-hybrid genotypes. Subsequently, however, cytologists have attempted to set up a series of precise, rigidly defined criteria for distinguishing between the two categories, based upon external morphology, morphological similarity of metaphase chromosomes, and presence or absence of multivalents at meiosis. They have then tended to place into the category of autopolyploids all plants which do not fit the definition of allopolyploids in respect to all the criteria mentioned above, and have concluded that in the evolution of these 'autopolyploids' hybridization has not played a significant role.

The weakness of this procedure is that it implies a much too narrow concept of hybridization. By focussing attention on the effects of crossing between widely different species, which can be easily separated by the taxonomist and which have chromosomes so different from each other that they do not pair at meiosis in the F_1 hybrid, it neglects the even more important and far more common effects on polyploidy of hybridization between closely related species or between ecotypes of the same species. A more realistic estimate of these effects can be obtained by adopting and applying a much broader concept of hybridization. This is the evolutionary concept, which has been defined as follows:²¹³ hybridization is crossing between individuals belonging to populations which have widely different adaptive requirements. On the basis of this definition, the parents of a hybrid may be conspecific, but belong to different ecotypes. In other instances they may belong to closely related species, to widely different species, or even to different genera.

Evaluation of criteria for distinguishing the kinds of polyploids

Before we can explore the implications of this definition of hybridization for our understanding of natural polyploidy, we must evaluate critically

the criteria which have been used for distinguishing between the different kinds of polyploids. A number of such criteria have been used, often uncritically, by authors of monographs as well as textbooks of cytogenetics. Too often, the assumption has been made that evolving populations will diverge from each other at equal rates with respect to a number of different, unrelated characteristics. This, however, is by no means the case. Often, evolutionary lines diverge from each other very widely with respect to morphological characteristics as well as ecological and geographic distribution, while retaining essentially similar patterns of chromosome morphology and segmental arrangement. In other instances, the external morphology of the chromosomes may remain very similar while chromosomal fine structure and gene contents diverge widely from each other.

Hybrid polyploids have been formed after crossing between populations having various degrees of divergence from each other with respect to these different characteristics. Moreover, occasional crossing between hybrid polyploids and one or both of their diploid ancestors, as well as intercrossing between polyploids having similar but not identical hybrid origin, has often complicated greatly relationships which originally were relatively simple. The next few pages are devoted to a documentation of these generalizations.

Because of this situation, any attempt to maintain a division of natural polyploids into two discrete categories, autopolyploids and allopolyploids, is more likely to confuse than to clarify a very complex system of interrelationships. In the present book, therefore, these two terms will be used only as ways of helping the reader to relate the present discussion of polyploids with those in other books.

The criteria which have been used are of two kinds: morphological, taxonomic characters as well as biochemical differences, all of which are the products of gene action; and cytogenetic differences, which affect directly the nature and segregation of the genes themselves.

External morphology and taxonomic key characters

The least reliable of these criteria is the assemblage of 'key characters' of external morphology which taxonomists ordinarily use in classification. The taxonomist is, rightly, most interested in ease of identification and classification. He is, therefore, reluctant to separate into different categories populations which cannot be easily differentiated by well defined characters of external morphology. These characters, however, express only a small fraction of the genetic differences between populations. Consequently, whenever wide-spread species are recognized by taxonomists are studied carefully, they are found to be highly heterogeneous genetically. This heterogeneity may be expressed partly in the form of different chromosome

numbers, which may be multiples of each other. In these instances, polyploid races or 'cytotypes' with higher chromosome numbers may often contain, in addition to the set derived from the name-giving 'cytotype' of the species, other sets derived from a completely different species. Because of various kinds of gene interaction, these foreign chromosomes may not have introduced into the 'cytotype' the key morphological characters by which taxonomists define the species from which they came, or may express these characters so weakly that they are not recognized.

A good example of this situation is the grass species, *Bromus arizonicus* (Fig. 5.3). This species was first described on the basis of the usual morphological characteristics, but its close resemblance to the wide-spread *B. carinatus* caused nearly all taxonomists to place it in synonymy until its cytological characteristics became known. In the most recent taxonomic treatment of the genus,²⁰⁰ it has been again relegated to the position of a 'cytotype' of *B. carinatus*.

There is, however, no doubt that half of the 84 chromosomes in the somatic cells of *B. arizonicus* have a completely different origin from any of the 56 chromosomes found in *B. carinatus*. This fact is evident both from a comparison of their karyotypes and from analysis of chromosome behaviour in the F_1 hybrid between *B. arizonicus* and *B. carinatus*. The gametic complement of *B. arizonicus* consists of 42 medium-sized chromosomes; that of *B. carinatus* contains 21 medium-sized chromosomes plus 7 much larger ones, which have no counterpart in *B. arizonicus*. In the F_1 hybrid, the 21 medium-sized chromosomes derived from *B. carinatus* are associated closely with 21 of the chromosomes derived from *B. arizonicus*, while the remaining chromosomes, both the 7 large ones derived from *B. carinatus* and the extra set of 21 derived from *B. arizonicus*, either remain as unpaired univalents, or pair only slightly with each other.

The only reasonable interpretation of this situation is that both *B. carinatus* and *B. arizonicus* are allopolyploids which share in common an ancestral species having the gametic set of 21 medium-sized chromosomes. The origin of *B. arizonicus* is from a hybrid between this common ancestral species and another one which also had 21 pairs of medium-sized chromosomes, while *B. carinatus* originated from hybridization between the same ancestor and a very different species having 7 pairs of large chromosomes. Further hybridizations have revealed the probable identity of the ancestral species concerned. The common parent probably belonged to the subgenus *Ceratochloa*, of which several 21-paired species occur in South America. The alternative 21-paired parent of *B. arizonicus* probably belonged to the subgenus *Neobromus*, while the 7-paired parent of *B. carinatus* belonged to the subgenus *Bromopsis*. Species belonging to both of these two subgenera differ from subg. *Ceratochloa* with respect to similar 'key characters',

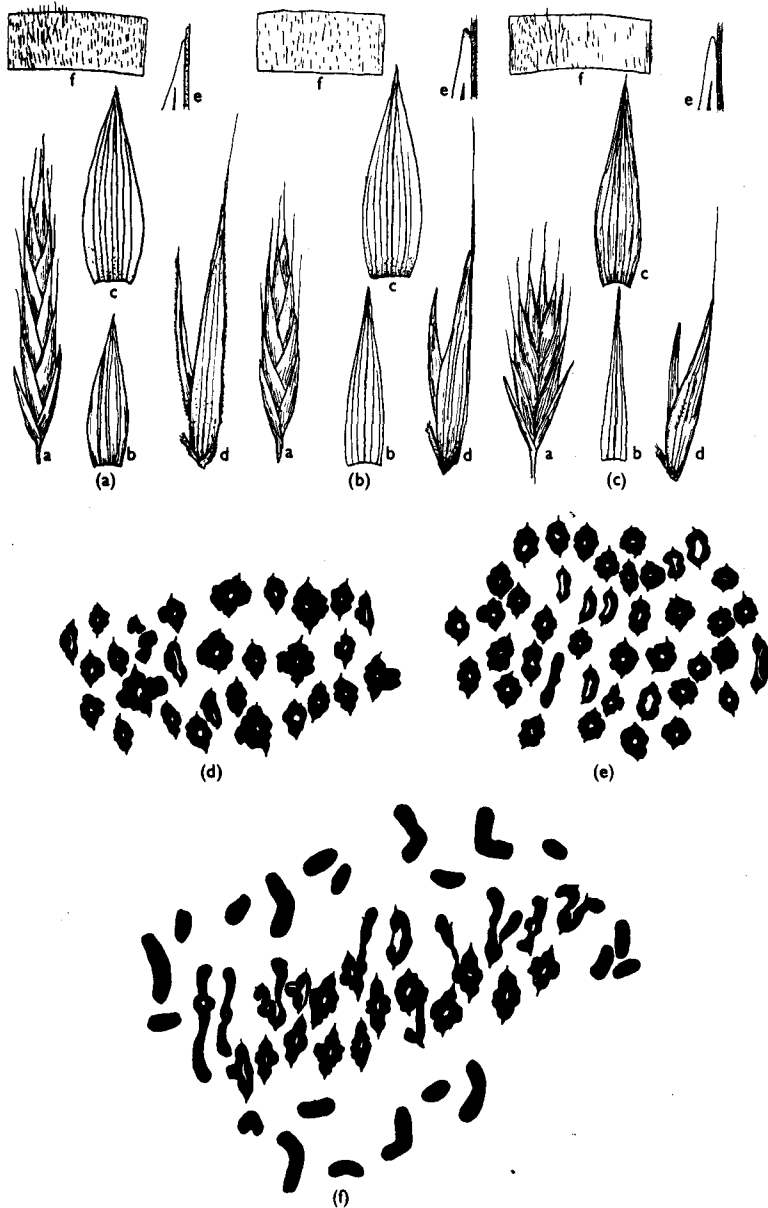


Fig. 5.3 Spikelet characteristics of *Bromus carinatus* (a), *B. arizonicus* (c), and their F_1 hybrid (b). Pairing of chromosomes in the two parental species (d, e) and the F_1 hybrid (f). (From Stebbins, Tobgy and Harlan.²²¹)

particularly lemmas rounded on the back and bearing long awns. The striking morphological differences between subg. *Bromopsis* and subg. *Neobromus*—awn bent *v.* awn straight; lemma bearing *v.* lacking prominent lateral teeth and marginal cilia—are in *B. arizonicus* so much diluted by the effects of the chromosomes derived from the *Ceratochloa* parent that they are difficult to recognize, and hence are not easily used as key characters by taxonomists.

Many similar examples can be cited: *Stipa pulchra* and *S. cernua*;¹⁵² the *Eupatorium microstemon* aggregate,¹⁰ and several examples in ferns. The morphological criteria used by taxonomists, although they must serve as the principal basis for distinguishing species in monographs and floras, are obviously inadequate guides to the evolutionary origin of many plant populations.

Biochemical differences

In recent years, various biochemical differences between populations have proved to be valuable aids in determining taxonomic relationships. Most frequently employed have been phenolic compounds,¹ seed proteins of an undefined nature,¹¹⁵ and isozymes of particular enzymes.¹⁹⁰ The advantage of these differences over the conventional morphological characters is that they can usually be determined with greater objective precision than can most of the morphological differences employed, which consist of complex shapes and configurations. Moreover, in the case of proteins, the differences being studied are more closely connected with differences with respect to particular genes than are morphological differences.

At present, the weakness of biochemical criteria is that only a few kinds of compounds can be studied by those who are not trained biochemists, and in many groups significant differences with respect to these compounds are not found. In the future, one may expect that these difficulties will gradually be overcome, so that the prospects are bright for an increasing usefulness of biochemical criteria. As is described later in this chapter, they have already been useful for analysing relationships within the polyploid complex of the genus *Lotus* (p. 143 and Table 5.2, p. 136).

Chromosome morphology

The morphology of somatic chromosomes at metaphase of mitosis has often been used as a criterion for distinguishing between 'autopolyploids' and 'allopolyploids'. In a tetraploid species, the chromosomes are matched with respect to gross characteristics such as length, position of centromeres, and of satellites. If they can be grouped only into pairs, the species is regarded as allopolyploid and consequently of hybrid origin; while if they

Table 5.2 Phenolic content of diploid and tetraploid members of the *Lotus corniculatus* complex. (From P. Harney and W. F. Grant⁹⁷).

Species	Origin	Chromosome number	Phenolic residues							
			D	Q	C	K	U ₁	pC	S	F
<i>L. corniculatus</i> L.	France	24	+	+	+	+	—	+	—	
<i>L. corniculatus</i> L.	France	24	+	+	+	+	+	+		+
<i>L. corniculatus</i> L. v. <i>ciliatus</i> Koch	Yugoslavia	24	+	+	+	+	+	+		+
<i>L. c.</i> var. <i>ciliatus</i>	Greece	24	+	+	+	+	+	+	+	+
<i>L. alpinus</i> Schleich.	Switzerland	12		+	+	+	+	+	+	+
<i>L. japonicus</i> (Regel) Larsen	Japan	12		+	+	+	+	+	+	+
<i>L. pedunculatus</i> Cav.	Austria	12	+	+	+	+		+	+	+
<i>L. pedunculatus</i> Cav.	Morocco	12	+	+	+	+		+		+
<i>L. pedunculatus</i> Cav. 4n	New Zealand	24	+		+	+		+		+
<i>L. tenuis</i> Waldst. & Kit.	Spain	12				+				+

can be grouped into sets of four, the species is regarded as autotetraploid, and not of hybrid origin.

The fallacy of this interpretation lies in the fact that metaphase chromosomes are simply the outer shells of the genetic material, and do not reveal their contents any more than the outer aspects of two identically designed suburban tract houses reveal the internal differences in their furniture, decorations, and the people inhabiting them. This fallacy is brought out clearly by detailed studies of the karyotypes belonging to species having large, easily distinguished chromosomes. In genera such as *Lilium*, *Trillium*, *Paeonia*, and *Bromus* subg. *Bromopsis* all of the species have similar karyotypes. Hence a tetraploid derived by chromosome doubling from any diploid hybrid in these genera will have metaphase chromosomes that can be grouped into matching sets of four, and so would pass as an autotetraploid according to this criterion. Nevertheless, most of the diploid hybrids which have been made between species of these genera have irregular meiosis and are highly sterile, showing that their chromosomes are well differentiated from each other in spite of their superficial similarity. In some instances, such as *Lilium tigrinum*,¹⁷⁵ careful studies of the details of chromosome morphology combined with hybridizations have shown that, contrary to earlier opinions which were based upon less careful comparisons, this triploid is most probably of hybrid origin, rather than an autotriploid derivative of a single ancestral species, as was previously supposed (Fig. 5.4).

In the case of genera having large chromosomes, and particularly chromosomes in which differential, allocyclic regions can be revealed by special treatments (cf. p. 35), comparative matching of metaphase

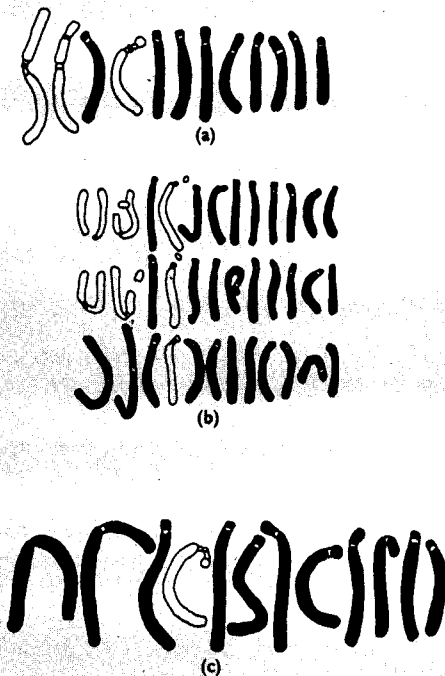


Fig. 5.4 Karyotypes of *Lilium tigrinum* and its probable progenitors. (a) From *L. tigrinum flaviflorum* ($2n = 24$), pollen grain mitosis. (b) From typical *L. tigrinum* (Hara, Japan), $2n = 36$, root tip. (c) From *L. Maximowiczii*, pollen grain. (From Noda.¹⁷⁶)

chromosomes can provide helpful though in no case decisive information concerning the origin of a particular polyploid. If, however, the chromosomes are medium-sized or small, this method should be used with great caution or not at all.

Multivalent formation

A criterion commonly used for distinguishing between ‘autopolyploids’ and ‘allopolyploids’ is the frequency with which chromosomes associate at meiosis into quadrivalents and trivalents instead of the usual bivalent association. The difficulties with using this criterion are twofold. In

the first place, even when four chromosomes are completely homologous with each other, they do not always form quadrivalents at first metaphase. Since at pachytene, chromosome segments associate only in two's, any one of four homologous chromosomes is associated with another particular homologue over only a part of its length. If chiasmata fail to form in these paired regions, the chromosomes will not remain paired at metaphase. Since chiasma frequency depends on chromosome length,⁴¹ polyploids in plants having small chromosomes are much less likely to form multivalents than those with large chromosomes. Furthermore, since chiasma frequency is in part genotypically controlled (p. 47), diploids which contain genes for lower chiasma frequency are likely to produce polyploids forming few or no multivalents.

On the other hand, the amount of chromosomal differentiation that is sufficient to build up a barrier of hybrid sterility between two species is far less than that required to prevent chromosomes from pairing in interspecific hybrids. This fact is evident from the existence of numerous interspecific hybrids which have good chromosome pairing at meiotic metaphase, but which nevertheless are highly sterile.²⁰⁹ A classic example is *Primula verticillata*-*floribunda*. When such hybrids are doubled, the derived polyploid usually has fewer multivalents than a polyploid derived from one of the parental species, because of preferential pairing (cf. p. 46).

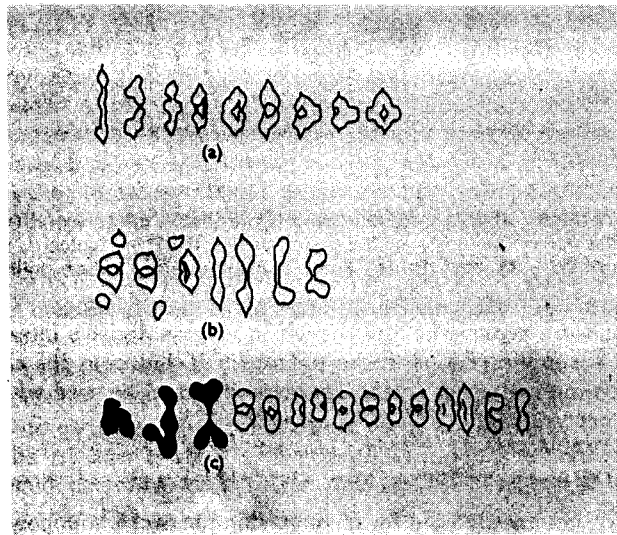


Fig. 5.5 Chromosome pairing at meiotic metaphase in *Primula verticillata* (a), *P. verticillata* x *floribunda* (b), and the hybrid polyploid, *P. kewensis* (c). (From Upcott.²³⁰)

Nevertheless, such hybrid polyploids often form multivalents, as in *Primula kewensis* (Fig. 5.5). They are, of course, more likely to do so if the chromosomes are large, and if chiasma frequency is high in the diploid parental species. The control of this multivalent formation by special genes is discussed elsewhere (p. 47).

One can conclude from these facts that the presence or absence of multivalent configurations in a natural polyploid may provide some indication as to whether or not it is of hybrid origin, but by itself this criterion is by no means decisive. It can be used only in connection with other cytological characteristics, as mentioned above.

Tetrasomic inheritance

A criterion which has often been used in tetraploids which have been intensively investigated genetically is the presence of tetrasomic inheritance for particular genes. If such patterns of inheritance are found, the plant is judged to be autotetraploid.

This criterion is certainly valid with respect to the particular chromosomal segment on which the gene is located. One must remember, however, that many tetraploids of hybrid origin can possess some chromosomal segments in quadruplicate, and others only in duplicate.

If disomic inheritance for a character is found in a tetraploid known to be of very recent origin, this is good evidence that the plant is of hybrid origin. On the other hand, most natural polyploids are old enough so that mutations which originated after the doubling had occurred could be well established in some populations. Hence disomic inheritance in a polyploid can indicate with equal probability either that the species is of hybrid polyploid origin, or that the gene difference in question has arisen recently. Consequently, the criterion of disomic *v.* tetrasomic inheritance is not a sufficiently reliable criterion of the origin of a polyploid to be worth the large amount of labour which is required to establish it.

Experimental hybridization and chromosome doubling

The most valuable criteria for determining the nature of origin of a polyploid can be obtained by a combination of carefully planned hybridizations and doublings of the chromosome number. An ideal scheme would be as follows. First, the diploid relatives of a particular polyploid should all be studied carefully, to find out which of them resemble it the most closely with respect to morphological, and if possible, biochemical characteristics. If the polyploid is suspected to be old and long established, this screening should be world-wide, since plant groups which have existed through the Pleistocene epoch have, during that time, undergone many alterations of their patterns of geographic distribution. Since a

polyploid is most likely to be successful if it is not competing directly with its diploid ancestor in the same habitat, we might expect to find often that well established polyploids would now be living in very different localities from those in which they originated, and where their diploid ancestors are still persisting.

Once these diploid relatives have been identified, they should be hybridized with each other, as well as with the polyploid under analysis. At the same time artificial polyploids should be obtained, with the use of colchicine, from both the species and their hybrids. Hybrids should then be made between the artificial polyploids and the natural one. The resulting polyploids and hybrids could be analysed and compared with respect to the criteria mentioned above: external morphology, biochemical characters, and chromosome association at metaphase. Such analysis should make possible a reasonably accurate hypothesis concerning the origin of the polyploid in question.

The importance of synthetic interpretations

The point cannot be over-emphasized that the interpretation of the origin of a polyploid, including the question of whether or not it is entirely or partly of hybrid origin, resembles all other interpretations of phylogeny. Its validity depends upon the strength of evidence derived from many different sources. Moreover, in constructing polyploid phylogenies, one cannot assume that the diploid ancestor or ancestors of a modern polyploid species still exist in their original form, unless good evidence for their existence has been obtained. Extinction or cytogenetic modification of diploid ancestors since they participated in the origin of a polyploid are likely possibilities that must always be taken into account. In the past, many erroneous interpretations of phylogeny have been made by morphologists, taxonomists and cytologists because they have fallen into one or both of the traps of reliance on only one kind of evidence and assumption that evolutionary ancestors of modern species still exist in an unmodified form. Interpretations of the nature and origin of polyploids have been no exception to this rule.

Kinds of polyploids at the primary level

In order to understand fully the facts now available about polyploidy and hybridization, we must recognize five different kinds of polyploids at the level of one cycle of chromosome doubling. This level usually involves one or more diploid ancestors and a series of tetraploids, but the same categories can often be recognized when the undoubled species are themselves of such ancient polyploid origin that they behave cytogenetically like diploids, such as the 'diploid' North American species of *Crepis*

discussed on p. 176, and the diploid species of *Malus*, *Crataegus*, and other members of the rose family with $x = 17$.

Non-hybrid polyploids

A few tetraploids belong to monotypic or ditypic genera that have no close relatives, and consist of one diploid and one tetraploid 'cytotype' which closely resemble each other. The example of *Galax aphylla* has long been known.²⁰⁹ Another example is *Achlys triphylla*⁷⁵ (Fig. 5.6). Both of these species are undoubtedly very ancient. They are members of the Arcto-Tertiary flora, which includes many groups that have evolved very little since the beginning of the Tertiary period, 60 million years ago. Both of them belong to families (Diapensiaceae, Berberidaceae) which contain many small genera that are very distinct morphologically and, like *Galax* and *Achlys*, belong to ancient, highly stable floras. These examples, therefore, support the general hypothesis that polyploidy is a stabilizing, conservative force in evolution. In spite of their great age, *Galax* and *Achlys* have been able to produce only polyploids which, morphologically and ecologically, are very much like their diploid ancestors.

Interecotypic hybrid polyploids

A number of polyploids have been recognized as products of chromosome doubling in a fertile hybrid between two different ecotypes of the same species. A good example is cocksfoot or orchard grass, *Dactylis glomerata*²²³ (Fig. 5.7). The races of this species which are predominant in Eurasia north of the Mediterranean region, and which have been extensively introduced into North America and other continents, are tetraploids. In both their morphological and ecological characteristics they are intermediate between two diploids which were described as distinct species, *D. Aschersoniana* and *D. Woronowii*. The former is strongly mesophytic, and is confined to forests, chiefly in central and northern Europe, although it also occurs in the mountains of south-eastern Europe. On the other hand, *D. Woronowii* inhabits semi-arid steppe country in south-western Asia. In respect to colour and texture of the leaves, as well as several morphological characteristics of their spikelets, *D. Aschersoniana* and *D. Woronowii* are strikingly different from each other. Typical *D. glomerata* is intermediate between them with respect to these characters as well as its habitat, which is more mesic than that of *D. Woronowii* and more sunny than that of *D. Aschersoniana*. The artificial hybrid between *Aschersoniana* and *Woronowii* is fully fertile and vigorous in both the F_1 and F_2 generations, so that these two entities, from the cytogenetic point of view, must be regarded as different ecotypes of the same species. Tetraploids produced artificially from

this hybrid closely resemble *D. glomerata* with respect to both their morphological characteristics and their production of many multivalents at meiosis. In addition to typical *D. glomerata*, there are many other tetraploid subspecies of the genus in southern Europe, North Africa, and western Asia, which in the same way combine various morphological and ecological characteristics of different diploid subspecies. The evolutionary success of intervarietal or interecotypic hybrid polyploids is often promoted by their hybrid vigour. This characteristic is buffered by the complexity of tetrasomic inheritance in their segregating progeny.

Interspecific hybrid polyploids

As has been mentioned earlier in this chapter, species that are well isolated from each other reproductively may be closely similar with respect to both the morphological appearance of their chromosomes and their structural patterns of chromosome segments. In other instances, the evolutionary divergence of species from each other involves profound repatterning of the chromosomes. Consequently, we should not expect to find that all polyploids derived from interspecific hybrids would resemble each other with respect to the morphological similarity of their chromosomes, the frequency of multivalents at meiosis, or the proportion of genetic differences which segregate according to the pattern of tetrasomic inheritance. Three modal situations will be described. Each of them is represented by a large number of natural polyploids.

The first of these is *Lotus corniculatus*. This tetraploid, which is common in western Eurasia and has been introduced as a forage plant in many parts of the world, was analysed many years ago as an autotetraploid,⁴⁴ and was then believed to be descended only from the diploid *L. tenuis*, which also occurs in western Europe. More recently, however, the section *Corniculatae* of *Lotus* has been found to contain four or more different diploid species, which can be recognized on the basis of slight morphological differences, occupy different geographical areas or ecological habitats, have distinctly different phenolic compounds, and can be intercrossed only with great difficulty^{88,89} (Fig. 5.8). Tetraploid *L. corniculatus* does not match any one of the diploid species on the basis of these characteristics, particularly the phenolic compounds (Table 5.2), and so probably contains genes derived from at least three or four of them.

The only way in which such interspecific hybrid polyploids can be distinguished from interecotypic hybrid polyploids is by identifying their diploid ancestors, and then finding out whether or not these ancestors can exchange genes freely. One must determine whether or not the diploids can easily be intercrossed, and whether or not their hybrids possess full fertility and vigour in both the F_1 and F_2 generations. This test has been

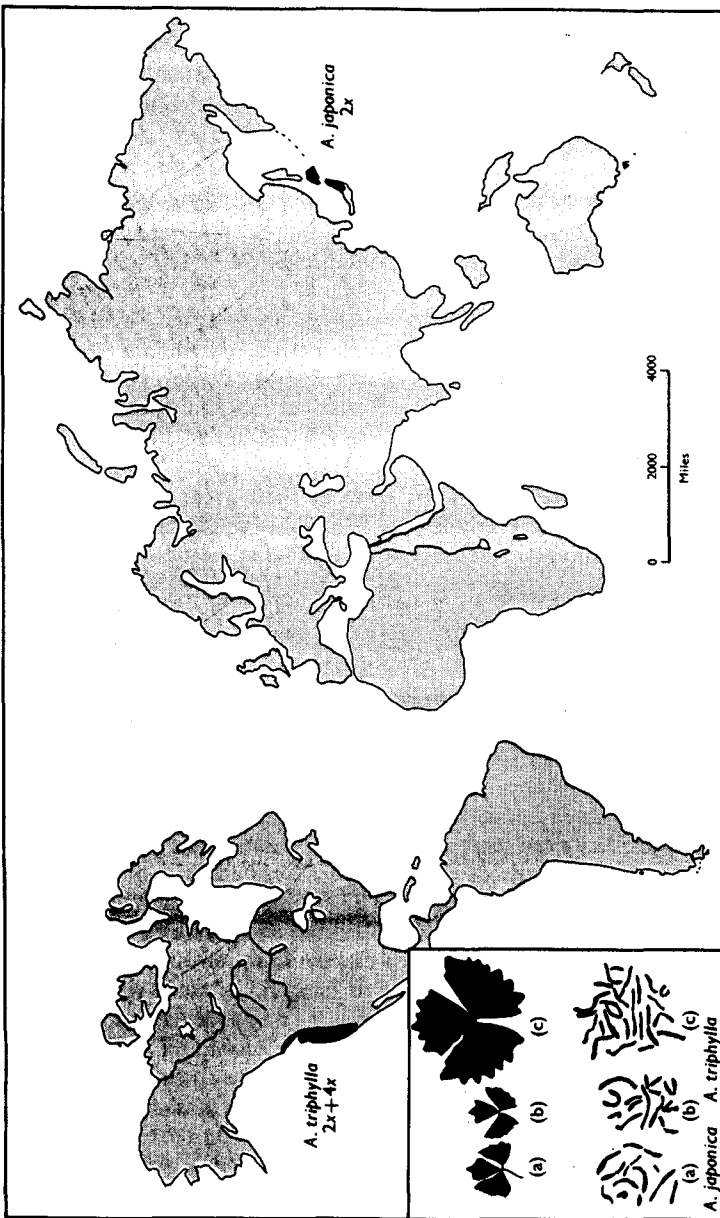


Fig. 5.6 Geographic distribution, outline of a typical leaf, and root tip chromosomes of *Achlys japonica* (a) and *A. triphylla*, $2x+4x$ (b and c). (From Fukuda.⁷⁶)

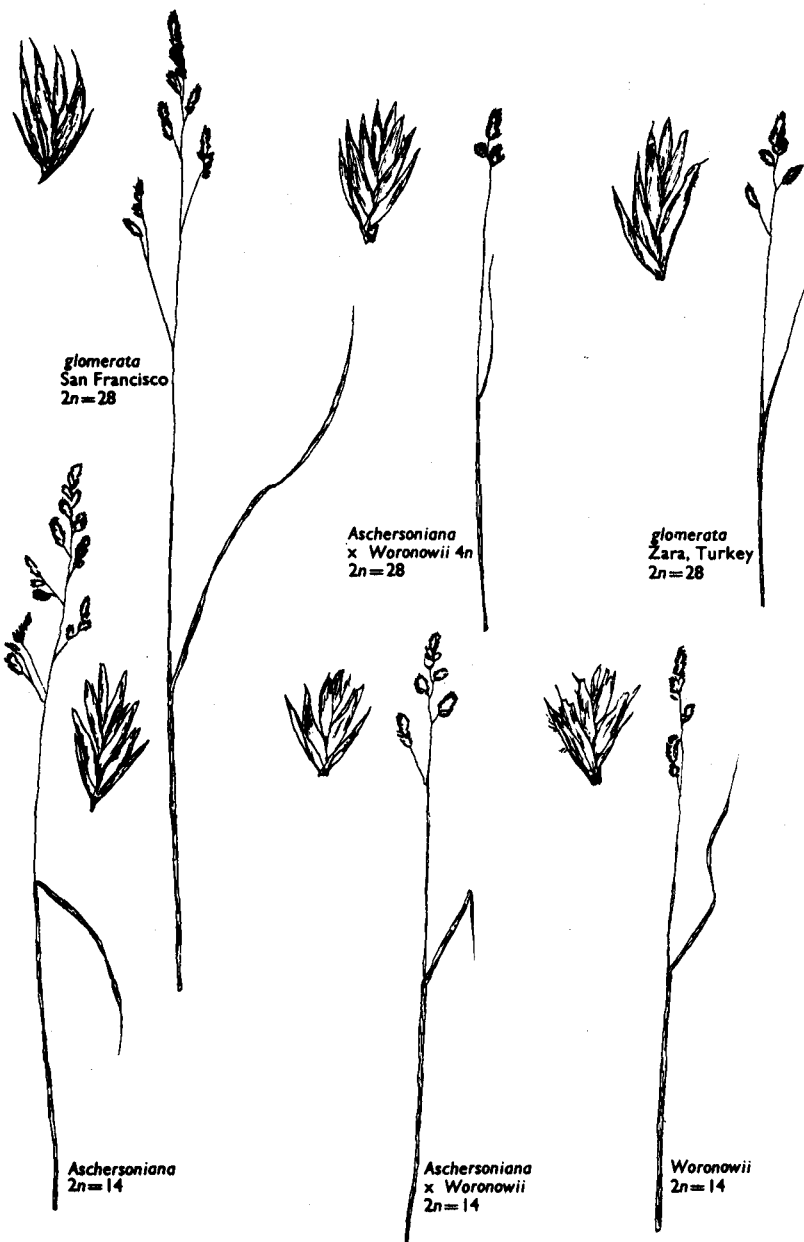


Fig. 5.7 Inflorescences and spikelets of two contrasting diploid subspecies of *Dactylis glomerata*, ssp. *Aschersoniana* and *Woronowii*, of the diploid F_1 hybrid between them, the doubled hybrid, and two tetraploid races of typical *D. glomerata*.

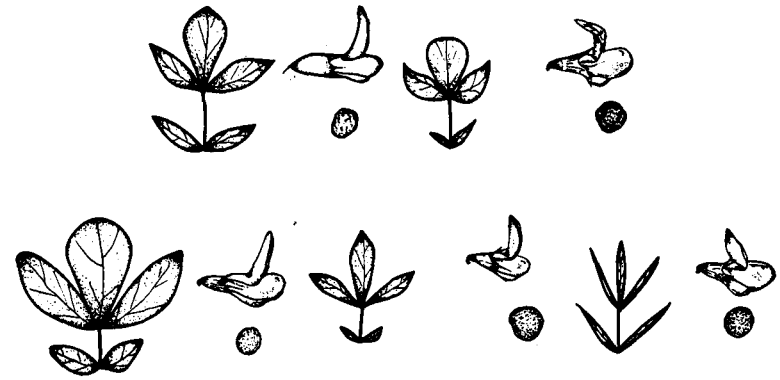


Fig. 5.8 Typical leaves, flowers and seeds of three diploid 'sibling species' of the *Lotus corniculatus* complex (lower row): *L. pedunculatus* (left); *L. Krylovii* (middle); and *L. tenuis* (right); and of two tetraploid races of *L. corniculatus* (top row). (From Zandstra and Grant.²⁵⁰)

performed in only a few genera. In addition to *Lotus corniculatus*, good examples are *Zauschneria californica*²⁰⁹ and tetraploid *Delphinium gypsophilum*.¹³⁸ Other probable examples are *Solanum tuberosum* and *Medicago sativa*. Well known tetraploids which are probably of hybrid origin but may be either interecotypic or interspecific, depending upon the undetermined relationships of their diploid ancestors, are *Biscutella laevigata*,²⁰⁹ *Campanula rotundifolia*¹⁷ and the tetraploid 'cytotypes' of such species as *Festuca ovina* and *Potentilla fruticosa*.

The second modal category is intermediate with respect to chromosomal differentiation. As was pointed out in the last chapter (p. 115), many species differ from each other with respect to numerous rearrangements (inversions, translocations) of chromosomal segments, but nevertheless are exactly alike with respect to gene arrangement over a large proportion and perhaps the majority of their chromosomal complements. Hybrids between such species will have reduced pairing and irregular meiosis, and preferential pairing in tetraploids derived from such diploid hybrids will result in the appearance at meiosis either only of bivalents, or of a few multivalents plus many bivalents. Tetraploids of this nature have been designated 'segmental allopolyploids'.²⁰⁹ A classical example is *Primula kewensis*. Naturally occurring examples are those which have recently evolved in eastern Washington between *Tragopogon dubius* and *T. porrifolius* as well as *T. pratensis*,¹⁷⁷ also *Knautia arvensis* and *Achillea collina*.⁶⁵ Perhaps the best known examples are the tetraploid and hexaploid wheats, in which bivalent formation and regular meiosis have been acquired secondarily through the action of certain genes (p. 117).

The hybrid polyploids with which cytologists are most familiar are derived from diploid hybrids between species of which the chromosomes have diverged from each other so much that little or no pairing between them is possible. Consequently the doubled hybrid forms exclusively bivalents at meiosis, and breeds true for intermediate morphological and ecological characteristics. The example of *Brassica oleracea*-*Raphanus sativus* has been widely cited in the literature of genetics and evolution. Other well known examples are *Galeopsis tetrahit*, *Nicotiana tabacum*, and the New World cottons (*Gossypium hirsutum*, *G. barbadense*, et aff.). Polyploids of this kind are designated in most monographs and textbooks as typical allopolyploids.

When the chromosomes of two or more ancestral species have become so strongly differentiated from each other that little or no pairing between them is possible, the gametic set of a particular diploid is inherited in derived polyploids as a single unit. Such units are termed *genomes*. In

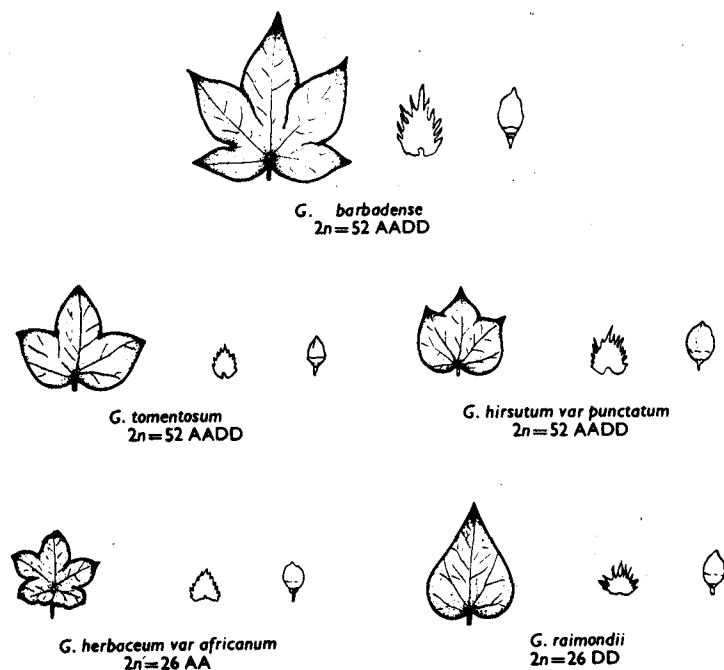


Fig. 5.9 Leaves, floral bracts, and capsules of three tetraploid species of cotton (*Gossypium*), and of modern relatives of their probable diploid ancestors. (From Stebbins.²¹⁴)

discussions of the phylogeny of a hybrid polyploid, the genomes are represented by a single capital letter. Thus the gametic set belonging to the Old World cultivated cottons, *Gossypium arboreum* and *G. herbaceum*, and their immediate wild relatives is designated A, and that belonging to wild species which contributed to the New World tetraploids is designated D. Hence somatic cells of the hybrid tetraploids carry the genomic formula AADD (Fig. 5.9).

Genomes are not, however, usually distinct, homogeneous categories. In many instances, two species may form a hybrid having perfect chromosome pairing at meiosis, indicating great similarity between their chromosomes. At the same time, hybrids between each of these species and a third species having an entirely different genome may differ from each other greatly in respect to chromosome pairing at meiosis.

In order to express minor differences between genomes, the letter symbols of them are often followed by modifying subscripts or superscripts. For instance, those of the different New World diploid species of *Gossypium* are usually designated D₁, D₂, etc. The fact that such modified symbols must be used emphasizes further the difficulty of maintaining a dichotomous 'either-or' kind of classification for natural polyploids.

The point must be emphasized that the modal categories just discussed are not sharply defined. Even when all facts about every natural polyploid become known, examples will exist which will be difficult to place into any one of them. They should not be regarded as completely separated compartments. Nevertheless, we can understand fully the relationship between hybridization and polyploidy only if we recognize a series of such modes.

SECONDARY MODIFICATIONS OF POLYPLOIDS

Most natural polyploids have existed for thousands or even millions of years, and have migrated from their locality of origin to many different parts of the world. During this time they have become secondarily modified and, in fact, modifications of various sorts have been essential to their success. Five different kinds of secondary modification have been important.

Mutation and genetic recombination

The theoretical reasons why mutation and gene recombination would not be expected to play as important roles in the evolution of polyploids as they do at the diploid level have already been given. Factual evidence to support this theory exists in the form of the variation patterns of many polyploid complexes. Very often, even in complexes which on the basis of

phytogeographical evidence must be regarded as hundreds of thousands or even millions of years old, the range of morphological variability encompassed by all of the tetraploids is less than the total range of that found among the diploids, except for the increased sizes of parts which are the direct result of chromosome doubling.

On the other hand, diversification at a particular level of polyploidy is particularly evident in groups which have maintained themselves at this level for long periods of time. In bringing about such diversification, mutation and gene recombination must have played important roles. The best examples are those of subfamilies or families which have basic chromosome numbers of polyploid origin, like the subf. Pomoideae of the Rosaceae.²⁰⁹

Chromosomal segregation

In polyploids descended from hybrids between closely related species, chromosomes derived from different parents can segregate more or less at random. We can follow the implications of this segregation by designating the chromosomes derived from one parent $a_1, a_2 \dots a_n$ and those derived from the other parents $a'_1, a'_2 \dots a'_n$, where n is the basic number of chromosomes. With respect to the centromeres and the chromosomal regions immediately adjacent to them, progeny from the original doubled hybrid can have for each chromosome five possible constitutions, $a_1 a_1 a_1 a_1$, $a_1 a_1 a_1 a'_1$, $a_1 a_1 a'_1 a'_1$, $a_1 a'_1 a'_1 a'_1$, and $a'_1 a'_1 a'_1 a'_1$. We might expect to find that natural selection would favour genotypes having a high proportion of a chromosomes in habitats similar to those occupied by the diploid a parent, and of a' chromosomes in habitats similar to those occupied by the a' parent. In this way, genetic segregation, recombination and natural selection, acting together on a hybrid autopolyploid which was advancing into a new territory, would produce a whole spectrum of genotypes and populations, encompassing the entire range of intermediacy from populations very similar to one of the original diploids in morphology and adaptiveness, through those similar to the original doubled hybrid, to populations resembling the other of the original parents. Because of the greater complexity of tetrasomic inheritance at the tetraploid level, each of these genotypes and populations would be more stable than corresponding ones at the diploid level. This stability could be further increased by the establishment of genes which would promote bivalent association and preferential pairing, thus reducing the amount of chromosomal segregation.

Just such a spectrum of morphological and ecological variants is known to exist in hybrid autopolyploids such as those of *Dactylis* and *Zauschneria*. In North America, for instance, where the diploid *Dactylis glomerata* ssp. *Aschersoniana* is absent, some forest areas, like the *Sequoia* forest of

north-western California, are inhabited by tetraploid races of *D.g.* ssp. *glomerata* which in their elongate, lax leaves and spreading, open inflorescences are much like ssp. *Aschersoniana*. On the other hand, tetraploid accessions of *D.g.* ssp. *hispanica* from Palestine, Turkey, and other parts of the Middle East, where they occupy open, dry steppe country, are so similar to the diploid ssp. *Woronowii* that they can be separated from that subspecies only on the basis of their chromosome number.

Unidirectional introgression

The phenomenon of *introgressive hybridization* or *introgression* is a sequence of three processes: hybridization, back crossing, and natural selection of back cross derivatives in a habitat where they are superior to either of the original parents. When introgression takes place between a tetraploid and a diploid population, there is a strong tendency for gene flow to proceed in only one direction, from the diploid to the tetraploid. This is for two reasons. In the first place, as demonstrated in *Dactylis*, when triploids occur as sporadic hybrids in populations containing both diploids and tetraploids, progenies of these triploids from open pollination consist largely of plants having either the tetraploid number or some number approximating it.²⁵² Secondly, many tetraploids and diploids are so highly cross-incompatible that triploid hybrids between them cannot be formed at all. Nevertheless, many diploid species produce a small proportion of unreduced diploid gametes, through rare failures of the meiotic process. Such gametes can unite with the normal diploid gametes produced by tetraploids to give rise immediately to vigorous, fertile tetraploid hybrids. In a normal outcrossing species all of the seeds produced by such hybrids will be the result of back crosses to their tetraploid parent. Although such hybridization is undoubtedly rare, it has been recorded in *Dactylis*, *Solanum*,¹⁶² *Grindelia*⁵⁸ and other genera. If the hybrids produced in this way, or their back cross progeny, were well adapted to a newly available ecological niche, such rare events could have evolutionary consequences far out of proportion to the rarity of their occurrence.

Evidence from variation patterns in nature suggests that unilateral introgression has played a highly significant role in increasing both the morphological range of variation and the ecological range of tolerance of many polyploids. The type of variation pattern which could have been produced most easily by this process is one in which a wide-spread tetraploid occurs sympatrically in different parts of its range with several different diploids, and in each region tends to possess races which resemble the diploids found in that particular region. This pattern is quite characteristic of *Dactylis*,²²³ *Knautia*,⁶⁵ *Grindelia*,⁵⁸ *Phacelia*,⁹⁹ *Campanula rotundifolia*,¹⁷ and many other groups.

Secondary hybridization

The most carefully worked out example of tetraploid species clusters are those of the grass genus *Aegilops*, studied by Daniel Zohary and his co-workers.²⁵¹ In the largest of these, the pivotal diploid parental species is *A. umbellulata*, a weedy annual found in the Middle East which possesses an unusually efficient method of seed dispersal in the form of a large number of beards or awns on its fertile scale or lemma (Fig. 5.10). Seven distinct tetraploid species contain a genome derived from *A. umbellulata*, which can be recognized both by the morphological characteristics which it introduces, as well as its distinctive karyotype (Fig. 5.10). The second genome found in these tetraploids is derived from ancestral diploids related to one of three different species complexes of *Aegilops*, those of *A. caudata*, *A. comosa*, and *A. speltoides*, which have been variously modified during later evolution at the tetraploid level. These tetraploids

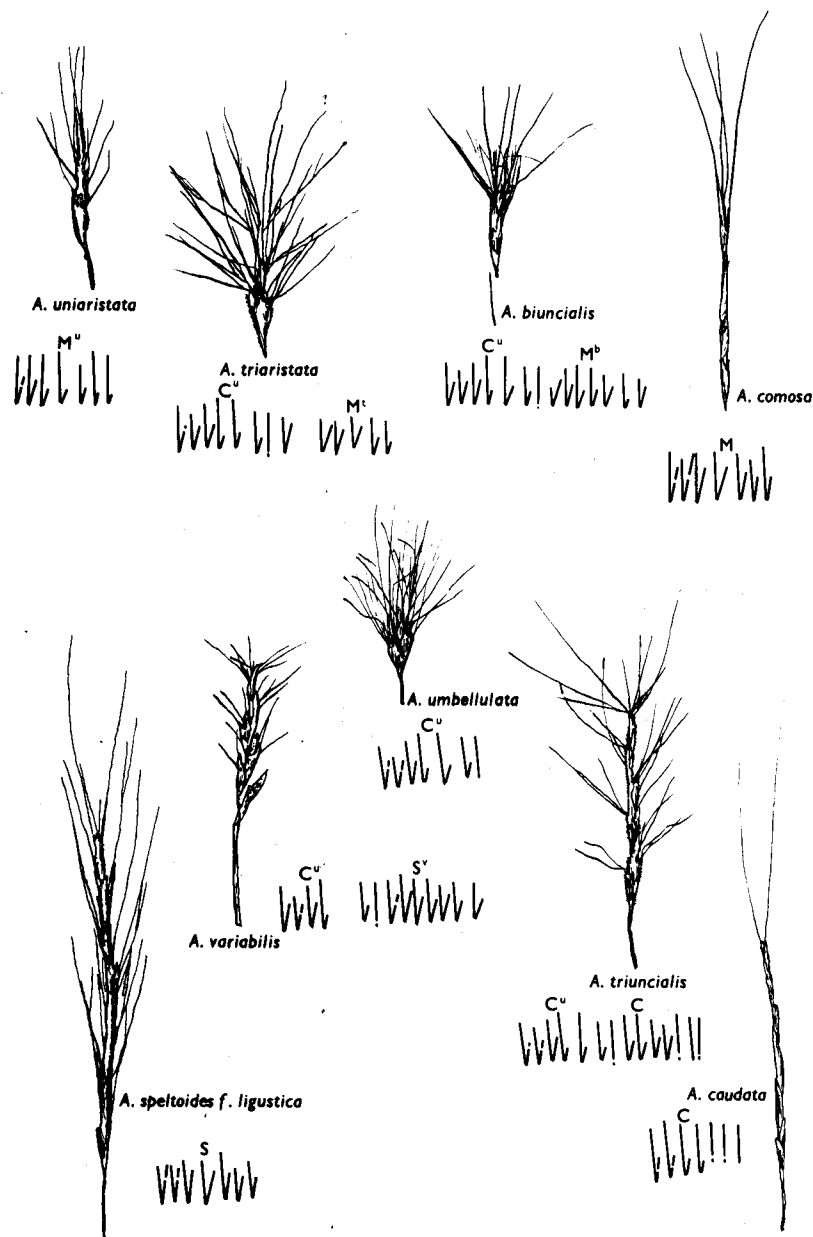


Fig. 5.10 Spikelets and karyotypes of four tetraploid species of *Aegilops* containing the pivotal genome C^a of *A. umbellulata* (centre) and of the four modern diploid species which contain counterparts of the other ancestral genomes: M^a, *A. uniaristata* (top left); M, *A. comosa* (top right); S, *A. speltoides* f. *ligustica* (bottom left); C, *A. caudata* (bottom right). The tetraploids are as follows: C^aM^a, *A. triaristata*; C^aM^b, *A. biuncialis*; C^aS^a, *A. variabilis*; C^aC, *A. triuncialis*. (Drawings of spikes made from photographs provided by J. Waines; karyotypes reproduced from figures of Chennaveeraiah.²⁶)

are all aggressive weeds, the most common of which have become widespread in the Mediterranean region. Two or more species are often found mingled together in the same habitat.

In these mixed populations hybrids are often found between two different tetraploid species. These plants can be recognized by their morphological intermediacy, by comparing them with artificial hybrids between the same two species, and by their low degree of fertility. They are completely pollen sterile, but set a small number of seeds from open pollination by the parental species. Progeny raised from such hybrids segregate widely, and recover almost complete fertility in one or two generations. Because of self pollination, which is predominant in these species as it is in most annual grasses, these fertile introgressed genotypes become fixed genetically with relative ease and, if they are of adaptive value, they may enlarge the ecological amplitude and increase the gene pool of the species concerned. The point must be emphasized here that self fertilization, although predominant in these species, is never complete, so that the introgressed genotypes, if they are interfertile with other individuals of the species concerned, may be regarded as part of its gene pool.

Secondary doubling

Occasionally, a hybrid tetraploid species may undergo a second doubling of its chromosome number to yield an octoploid, which now has two genomes, each present four times. If, according to the usual practice, the original gametic chromosome sets are designated A and B, the allotetraploid has for its somatic complement the formula AABB and the octoploid derived from it AAAABBBB. Cytogenetically, such a polyploid shows a combination of autopolyploid and allopolyploid characteristics. The best known example is the California blackberry, *Rubus ursinus*. Its unusual genomic constitution is responsible for the ease with which it can form fertile hybrids by outcrossing to distantly related species. For instance, the loganberry arose as an accidental hybrid in a garden where a female plant of this dioecious species was exposed to pollen of a diploid raspberry

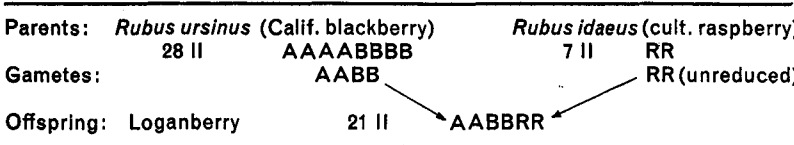


Fig. 5.11 Diagram showing how the hexaploid, fertile and stable cultivated loganberry probably originated through natural crossing between the octoploid California blackberry and an unreduced diploid pollen grain produced by the diploid raspberry.

which contained some unreduced gametes. As a result, the reduced egg of the blackberry, containing the genomes AABB, united with a raspberry pollen grain carrying RR, and the fertile hexaploid, AABRR, was the result²⁰⁹ (Fig. 5.11).

This type of secondary doubling is, however, relatively uncommon, and has not played a major role in the evolution of polyploid complexes. One reason for this is that two cycles of doubling, unaccompanied by hybridization, usually give rise to weak, abnormal plants, as in *Nicotiana*.⁹¹

Secondary hybrid polyploidy

A much more important secondary source of variability for polyploid complexes is hybridization followed by additional chromosome doublings. In some instances, a hybrid tetraploid is outcrossed to a third species, and the resulting triploid is doubled to produce a hexaploid which contains chromosomes derived from three original diploid species. The origin of the hexaploid bread wheats (AABBDD) from hybrids between the tetraploid emmer or macaroni wheats (AABB) and *Aegilops squarrosa* (DD) is a familiar example. In other instances, a tetraploid may be back crossed to one of its ancestral diploids, and the resulting triploid hybrid may become doubled to produce a hexaploid having twice as many chromosomes derived from one of its parents as from the other. The origin of hexaploid *A. crassa* C^uC^uM^tM^tM^{t2}M^{t2} from the more wide-spread tetraploid of that species, C^uC^uM^tM^t, is a good example. In general, hexaploids of this kind are so similar to their ancestral tetraploids that the two are often placed in the same taxonomic species. This procedure is justifiable on the grounds that hybridization between tetraploids and closely related hexaploids can usually occur in nature when the two forms occur together and the resulting pentaploid hybrids, although they are highly sterile, can nevertheless often produce introgressed genotypes through back crosses with either of the parental species. The similarity between these forms is, therefore, based partly upon their sharing many genes originally, and partly upon subsequent gene exchange.

When secondary hybridization and polyploidy take place, the relationship between the parents of the second combination may be quite different from those which formed the first tetraploid. Thus, an interecotypic hybrid polyploid may cross secondarily with a closely related diploid, to produce a hexaploid having three genomes which are largely but not completely homologous with each other. On the other hand, it may cross with a distantly related species, to produce a bigenomic hexaploid, AAAABB. The number of possible situations is very large, and the complexity can be increased through pairing and crossing over between chromosomes belonging to partly differentiated or homoeologous genomes.

Consequently, at levels higher than tetraploidy, the 'autotetraploid' and 'allotetraploid' conditions can become so much mixed and combined with each other as to render any attempt to classify such secondary polyploids into clearly defined categories futile and meaningless.

THE POLYPLOID COMPLEX AS AN EVOLUTIONARY UNIT

A much more meaningful way of looking at the more complex products of hybridization and polyploidy is to regard them as members of a *polyploid complex*, and to study such complexes as units in themselves. Emphasis is then placed upon the processes which take place in their origin and evolution, rather than in classification and categorization of individual polyploids or groups of them. A more or less idealized diagram of a polyploid complex is presented in Figure 5.12. The theme of the next chapter will be the evolution of polyploid complexes, and its relation to ecology, plant geography, and broader questions of evolution in general.

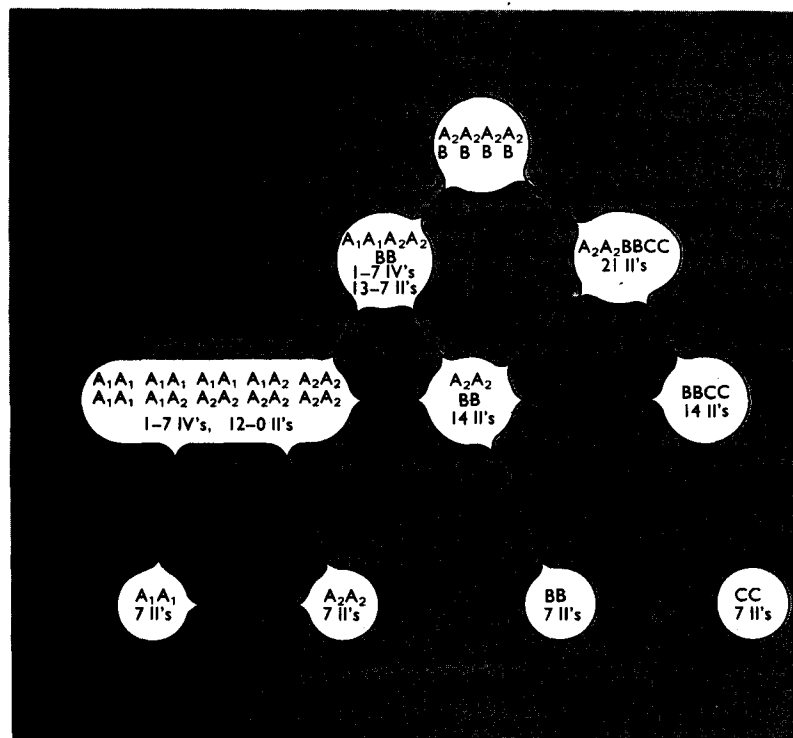


Fig. 5.12 Diagram showing a typical polyploid complex, and the various ways in which it can evolve by hybridizations and chromosome doublings.

6

Polyploidy, Plant Geography, and Major Trends of Evolution

From the material presented in the last chapter, we can conclude that polyploidy combined with hybridization has exerted a major influence on the evolution of higher plants. Its effects have been conservative. Hybridization has drastic effects on populations, since it inevitably results in the appearance of radically new gene combinations. Most of these combinations are inadaptable in any habitat. Furthermore, in a stable environment in which no ecological niches are open to colonization, all of the combinations generated by hybridization are likely to be less adaptive than those of the parental races or species, and so to be discarded by natural selection. On the other hand, when the products of hybridization are exposed to a rapidly changing environment, in which many new ecological niches are being opened up, some of these new combinations are highly likely to be better adapted to these new conditions than are any genotypes present in the old established populations. Polyploidy serves the purpose of stabilizing these valuable new genotypes, both by reducing the amount of genetic segregation, and by eliminating the sterility which exists in hybrids between well differentiated species. In addition, many individual polyploid genotypes have phenotypes which are able to tolerate a wide range of environmental conditions: they are 'general purpose genotypes'.⁹ The increased size of certain organs, particularly seeds, which accompanies polyploidy may also help in the process of stabilization and establishment in new habitats, since it increases seedling vigour.