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Chapter 6

Polyploidy, Plant Geography, and Major Trends of Evolution

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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 inadaptive 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.

The purpose of the present chapter is to review our knowledge about the comparative distribution of diploids and related polyploids in the light of the generalizations presented in the last paragraph, and to make whatever inferences seem to be justified about the effect of polyploidy on plant evolution.

CHARACTERISTICS OF POLYPLOID COMPLEXES

Reversibility of polyploidization

Polyploidy is predominantly an irreversible trend from lower to higher levels. This irreversibility is due not to the genetic impossibility of reversal, but to either the lowered overall adaptability or the evolutionary insignificance of its products. In the tribe Andropogoneae of the grass family, De Wet^{52,53} has shown that natural autopolyploids can give rise to diploid populations. Successful reversions of this sort, however, occur only in autopolyploid populations which appear to be of relatively recent origin, and which are living sympatrically with their diploid progenitors. Such reversions do nothing more than add to the already large gene pool of the diploids, and to retard the divergent evolution of the tetraploids. Older tetraploids, which have spread beyond the range of their diploid ancestors and through the various processes already described have evolved new genotypes, invariably are either incapable of producing viable diploid offspring, or the revertants are weak, sterile, or both. This is because both mutation and the various forms of secondary hybridization and introgression tend to convert gene loci from the tetrasomic to the disomic condition. When this has happened, the diploids derived from the modified tetraploid are monosomic at many gene loci, a condition which gives rise to their weakness or sterility.

Since effective trends of polyploidy are from lower to higher levels, polyploid complexes are particularly useful for analysing problems of plant geography and phylogeny. Although they have often been used for this purpose, their possibilities in this direction have by no means been fully exploited. The relation of polyploidy to plant geography and phylogeny is a very fruitful field for further investigations.

Divergent trends in diploids and polyploids

As suggested in the last chapter, the processes of mutation and gene recombination are more effective in the evolution of diploids than of polyploids. As a result, radically new adaptive complexes, such as new floral structure, methods of pollination, and seed dispersal, are much more

likely to evolve at the diploid level than in polyploids. On the other hand, the great ecological amplitude which polyploid species can acquire gives them a high degree of buffering against the environmental changes which take place over long periods of time, due to glaciations, mountain building and degradation, and overall fluctuations in the earth's climate. These factors lead to entirely different evolutionary patterns among the polyploid members as compared to the diploid representatives of any particular polyploid complex.

As the polyploid complex becomes older, its diploid members are likely to become progressively more restricted in geographic distribution and finally extinct. The only exceptions are those which evolve adaptive combinations and chromosome structures which are so radically different from those possessed by the ancestors of the polyploids that they place these newly evolved diploid populations beyond the recognizable limits of the polyploid complex.

The polyploid members, on the other hand, enlarge their gene pools and geographic distributions in the ways already described, and, as they invade the geographic areas of additional diploids, acquire genes from them. In this way they build up entities termed *compilospecies*.⁵⁴ These are wide-spread systems of polyploid populations which include chromosomes and genes derived from many different diploids, all of which are incorporated into a system within which free gene exchange is possible. The compilospecies centering about the grass species *Bothriochloa intermedia* is distributed throughout the Old World tropics and neighbouring warm temperate regions.⁵⁴

This differential evolution gives rise to a correlation between the age of a polyploid complex and the relative abundance of its polyploids as compared to their diploid ancestors. On the basis of this criterion we can recognize five stages of maturity: (1) initial, (2) young, (3) mature, (4) declining, (5) relictual.

Initial polyploid complexes

In their initial stages, polyploid complexes consist of one to several wide-spread diploid species within the distributional ranges of which are found one or more restricted areas occupied by polyploids. The best example is that of the three species of *Tragopogon*, *T. porrifolius*, *T. pratensis*, and *T. dubius*, described by Ownbey¹⁷⁷ (Fig. 6.1). In their native range in Eurasia, all three of these species are diploids having six pairs of chromosomes, and no polyploid species of *Tragopogon* are known from the Old World. In North America, *T. porrifolius* has been introduced on the west coast of the United States, from Washington to California, while *T. pratensis* is established in cool climates all across the continent. The

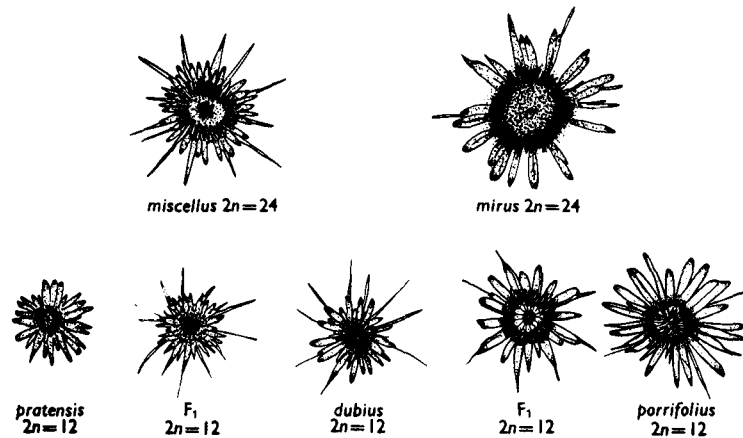


Fig. 6.1 Flowering heads of three diploid species of *Tragopogon* (bottom row); *T. pratensis* (left), *T. dubius* (centre) and *T. porrifolius* (right), and of F_1 hybrids which led to the polyploid hybrid species *T. miscellus* (top row, left) and *T. mirus* (top row, right). (From Ownbey,¹⁷⁷)

introduction of *T. dubius* is chiefly in the mountain states. No species of *Tragopogon* is native to the New World.

Allopolyploids between *T. porrifolius* and *T. dubius*, as well as *T. pratensis* and *T. dubius*, were first found in south-eastern Washington, in 1949, where the parental species had been introduced for only about 25 to 30 years. The exact age of the polyploids is unknown, but their recent spread is being carefully followed (Fig. 6.2).

Young polyploid complexes

The best example of a young polyploid complex is that of *Aegilops*, described in the last chapter (p. 150). The pivotal diploid species of the C^u cluster, *A. umbellulata*, is still wide-spread both as a weed and in semi-natural habitats. Its range overlaps with those of the three other diploid species which contributed genomes to the tetraploids, *A. caudata*, *A. comosa*, and *A. uniaristata*, so that some degree of sympatry exists between all of its species, both diploid and tetraploid (Fig. 6.3). On the other hand, the tetraploid species *A. triaristata* and *A. triuncialis* have spread far beyond the limits of all of the diploids, and are far more aggressive and weedy. Since they occur exclusively in habitats which have been greatly modified by human activity, the most logical conclusion is that this complex began its evolution together with the beginnings of agriculture and the grazing of domestic animals, about 10 000 years ago.

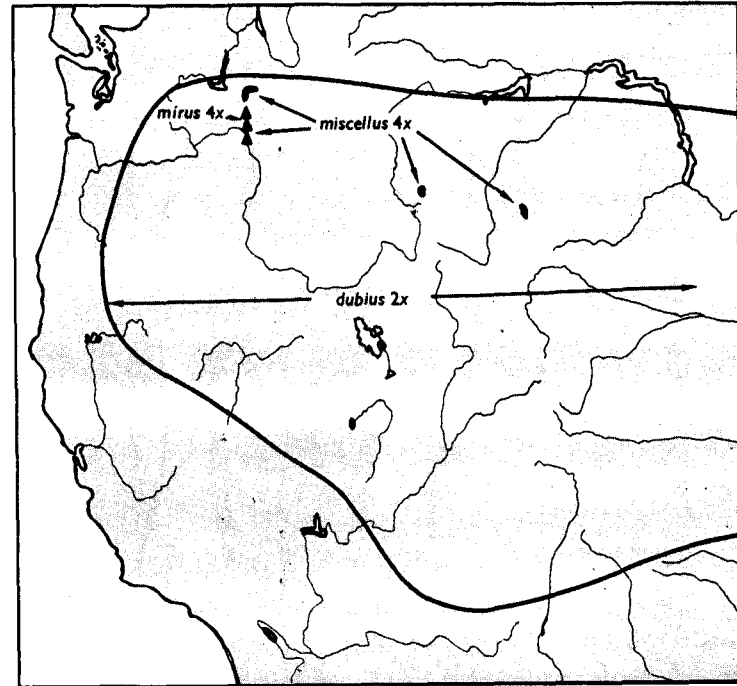


Fig. 6.2 Occurrence, generalized, of the European diploid species *Tragopogon dubius* as a naturalized weed in the western United States, and localities where its hybrid polyploids with *T. pratensis* (*T. miscellus*) and *T. porrifolius* (*T. mirus*) have been found. The diploid species *T. pratensis* is extensively naturalized throughout the area of *T. dubius*, while *T. porrifolius* occurs chiefly in the western part of the area. (From unpublished data of Marion Ownbey.)

The complex of *Lotus corniculatus*, described in the last chapter, can be regarded as intermediate between youthful and mature. Its diploid representatives are still numerous and wide-spread, although they are rarely sympatric with each other, and have diverged genetically to such an extent that diploid hybrids can be made only by artificial means. The total natural range of all of the diploids still exceeds that of the tetraploids. Nevertheless, in most of western Europe, particularly in those regions which were covered or much altered by the Pleistocene glaciation, the tetraploid *L. corniculatus* is by far the most common, dominant member of the complex.

Mature polyploid complexes

This category includes the great majority of described polyploid

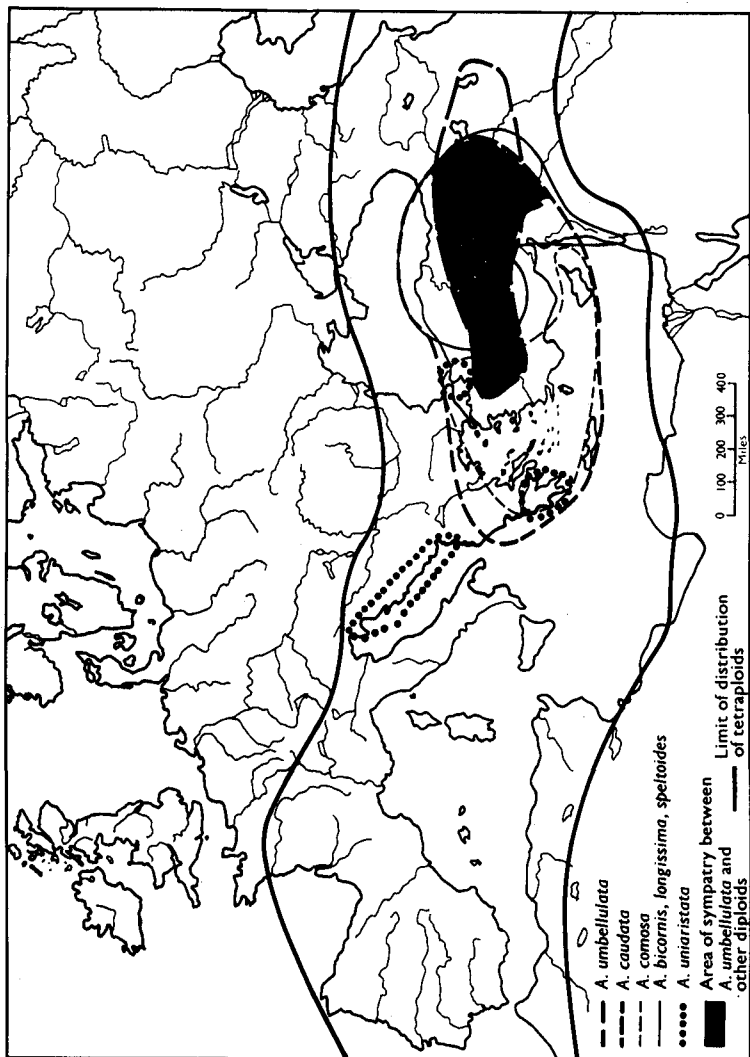


Fig. 6.3 Map of the Mediterranean region, showing the distribution of the diploid species which have entered into the *Agilops umbellulata* polyploid complex, and the limits of distribution of the tetraploid members of this complex. (Data from Fig. 87)

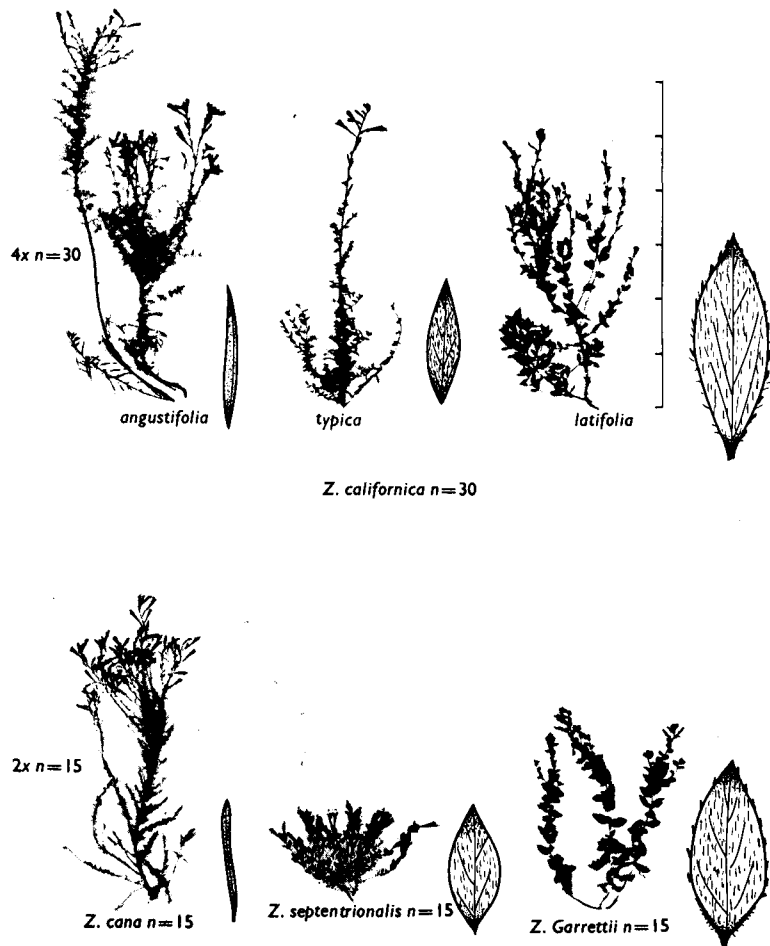


Fig. 6.4 Outlines of the growth habit and leaves of the three diploid representatives of the *Zauschneria* polyploid complex (Onagraceae), *Z. cana*, *Z. Garretti*, and *Z. septentrionalis*, and of three subspecies of the tetraploid *Z. californica*. Hybrids between the diploids are vigorous and fertile, but their progeny degenerate in the F_2 and later generations. The tetraploids are freely able to exchange genes with each other. (From Clausen, Keck, and Hiesey.³³)

complexes. In them, both the morphological and ecological extremes are usually represented by diploids. These are, however, much less extensively developed than the polyploids. Their geographic ranges are more restricted, and the amount of genetic variation within their populations is usually

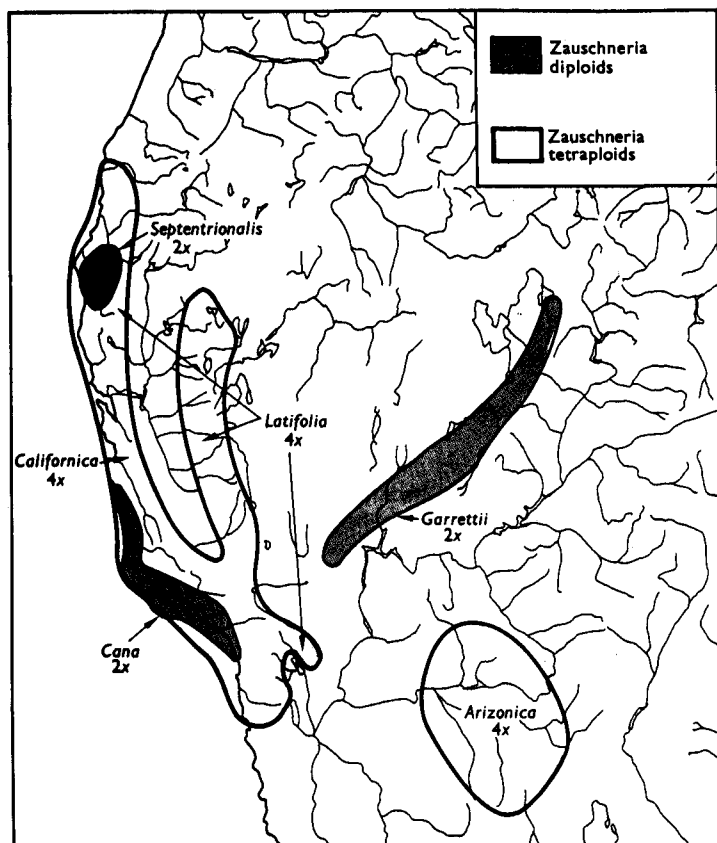


Fig. 6.5 Map of the western United States, showing the distribution of the diploids and tetraploids of the *Zauschneria* polyploid complex.

less. Furthermore, their diploids are usually allopatric with each other or sympatric in only restricted areas, so that hybridization and doubling involving different diploids has become impossible.

Several examples of mature polyploid complexes have already been described. The genera *Zauschneria* (Figs. 6.4 and 6.5) and *Dactylis* are representative of complexes which with respect to the chromosome numbers involved are relatively simple. Table 6.1 lists several other examples. In the great majority of mature polyploid complexes, the most

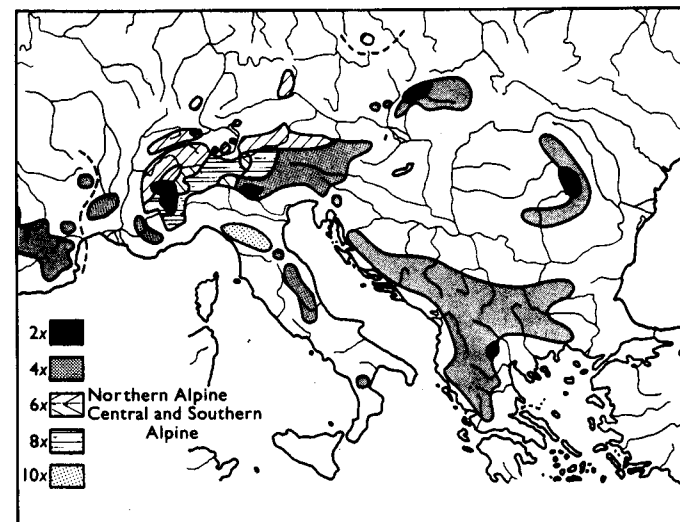


Fig. 6.6 Map showing the distribution of the polyploid complex of *Galium anisophyllum* in central and southern Europe. The diploids occur in widely separated portions of the Alps, the mountains of Central Europe and the Balkans, in which the effects of Pleistocene glaciation were minimal. The tetraploids are more wide-spread than other chromosomal levels. Hexaploids and octoploids occur chiefly in the glaciated portions of the Alps and Pyrenees. Finally a decaploid subspecies of *Galium anisophyllum* occurs in the northern Apennines of Italy. (From Ehrendorfer.⁶⁵)

wide-spread level of polyploidy is tetraploid. Hexaploids and octoploids, when present, are both fewer in number and more restricted in distribution. There are, however, some exceptions to this generalization. One of them is in the genus *Galium*. In Europe, the complex of *G. anisophyllum* consists of diploids, tetraploids, hexaploids, octoploids, and decaploids, of which the tetraploids are the commonest and most wide-spread (Fig. 6.6).

Most of the polyploid complexes in which levels higher than tetraploidy are predominant appear to have gone through two or more cycles of polyploidy, with periods of diversification and differentiation at the diploid or tetraploid level before the higher polyploids appeared. They are discussed in a later section of this chapter (p. 193).

An aneuploid complex: Claytonia in eastern North America

One of the most extensive series of chromosome numbers found in any groups of closely interrelated populations exists in the spring beauties,

Table 6.1 Representative sexual polyploid complexes. Y—Youthful complexes; abundance and diversity of diploids nearly equalling to exceeding tetraploids. M—Mature complexes; diploids less wide-spread than tetraploids.

Name of Complex and Reference	Basic number	Levels of polyploidy	Geographic Distribution Diploids	Geographic Distribution Polyploids	Occurrences of sympatry Between different diploids	Occurrences of sympatry Between diploids and polyploids
<i>Artemisia tridentata</i> (Y) Ward, ²³⁷ Beetle, ¹⁴ Taylor <i>et al.</i> ²²⁸	$x = 9$	4x, 6x, 8x	Western North America	Similar	Wide-spread	Wide-spread
<i>Galium multiflorum</i> (Y) Ehrendorfer, ⁶³ Dempster and Ehrendorfer ⁵⁰	$x = 11$	4x, 6x	Deserts and mountains of western U.S.	Siskiyou Mountains, Sierra Nevada, southern Great Basin	Southern part of range	Similar
<i>Gayophytum</i> spp. (Y) Lewis and Szweykowski ¹⁴¹	$x = 7$	4x	Western U.S., temperate South America	Western North America, temperate South America	Throughout range of diploids	Similar
<i>Tradescantia virginica</i> (Y) Anderson and Sax, ³ Anderson, ² Dean ⁴⁸	$x = 6$	4x	Central and southern U.S.	Rocky Mountains—Atlantic, south to northern Mexico	Central Texas	Throughout range of diploids
<i>Achillea millefolium</i> (M) Clausen, Keck and Hiesey, ³⁴ Ehrendorfer, ⁶⁰ Schneider ¹⁹¹	$x = 9$	4x, 6x, 8x	Central and southern Europe, south-west Asia	Eurasia, North America	Central Europe	Similar
<i>Campanula rotundifolia</i> (M) Guinochet, ⁹⁴ Bøcher, ¹⁸ Hubac, ¹⁰⁶ Gadella ⁷⁹	$x = 17$	4x, 6x	Alps, Pyrenees, central and northeastern Europe, Arctic regions	Eurasia, North America	Not known	Alps, Pyrenees, Greenland
<i>Clarkia rhomboidea</i> (M) Mosquin ¹⁶⁸	$x = 7, 5$	4x (2x, 2x)	Mountains of northern and central California	Western North America	None	Throughout range of diploids
<i>Drosera anglica</i> (M) Wood ²⁴⁷	$x = 10$	4x	Holarctic	Similar, plus Hawaii	Northeastern North America	Wide-spread
<i>Fragaria</i> spp. (M) Dogadkina, ⁵⁶ Staudt ^{203, 204, 205}	$x = 7$	4x, 6x, 8x	Eurasia, North America	Eurasia, North and South America	Western Eurasia	Throughout most of diploid range
<i>Gilia</i> sect. <i>Arachnion</i> (M) Grant and Grant, ⁸⁴ Day ⁴⁵	$x = 9$	4x	Deserts of south-western U.S.	Similar	None between progenitors of tetraploids	Portions of range of diploids
<i>Phacelia magellanica</i> (M) Heckard ⁹⁸	$x = 11$	4x	Western U. S.	Western North America, South America	Northern California	Through most of diploid range
<i>Rumex paucifolius</i> (M) Löve and Sarkar, ¹⁵¹ Smith ¹⁹⁸	$x = 7$	4x	Southern Sierra Nevada, north central Rocky Mountains	Mountains of western U.S.	None	Through most of diploid range
<i>Sanicula crassicaulis</i> (M) Bell ¹⁵	$x = 8$	4x, 6x	Coastal and southern California	Pacific North America, South America	South central California	Throughout diploid range

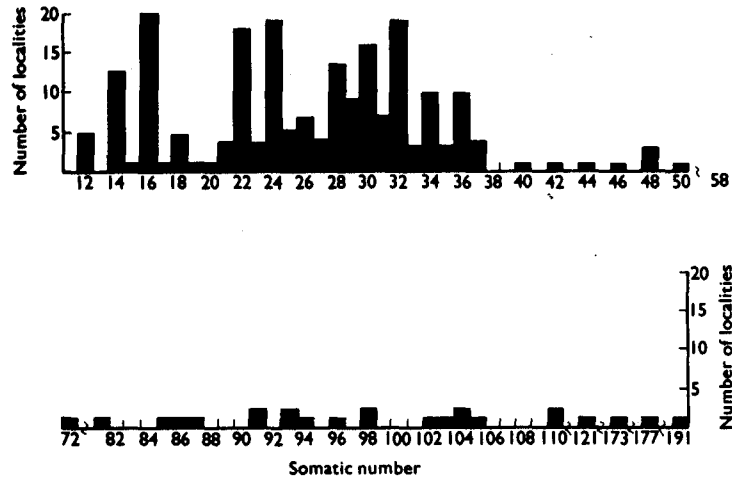


Fig. 6.7 Frequency distribution of the different chromosome numbers found within the single species *Claytonia virginica*. Owing to the fact that the central and southern portions of the range of the species have been sampled much more intensively than the northern and north-eastern regions, the sample may not be completely representative, but it is unlikely that many additional numbers will be found. The reproductive biology and seed fertility of the different chromosomal races have not been recorded. (From Lewis, Oliver and Suda.¹⁴²)

genus *Claytonia*, of eastern North America. In *C. virginica* there are diploids with $n = 6, 7,$ and 8 , which occur in localized portions of the south-eastern United States, in Tennessee, Alabama, Missouri, Arkansas, and Texas¹⁴² (Fig. 6.7). The related species *C. caroliniana*, found principally in the Appalachian region and northward into New York, New England, southern Canada, and the Great Lakes region, consists chiefly of diploids with $n = 8$. In both species, polyploid cytotypes have been reported, but the series is by far the most extensive in forms referred to *C. virginica* (Fig. 6.8). The maximum number, $2n = \pm 191$,¹⁸⁸ must be regarded as the 24-ploid condition.

In contrast to most polyploid complexes, aneuploidy is general within *Claytonia*. Two reasons can be given for this anomaly. In the first place, the original diploids may once have been more wide-spread than they are now, and therefore could have occurred sympatrically and hybridized with each other. From different combinations between them tetraploids could have appeared having every number from $n = 12$ to $n = 16$, and hexaploids having every number from $n = 18$ to $n = 27$. Further inter-crossings between races and subsequent doublings could have built up the higher series of aneuploid numbers. Secondly, because of the high

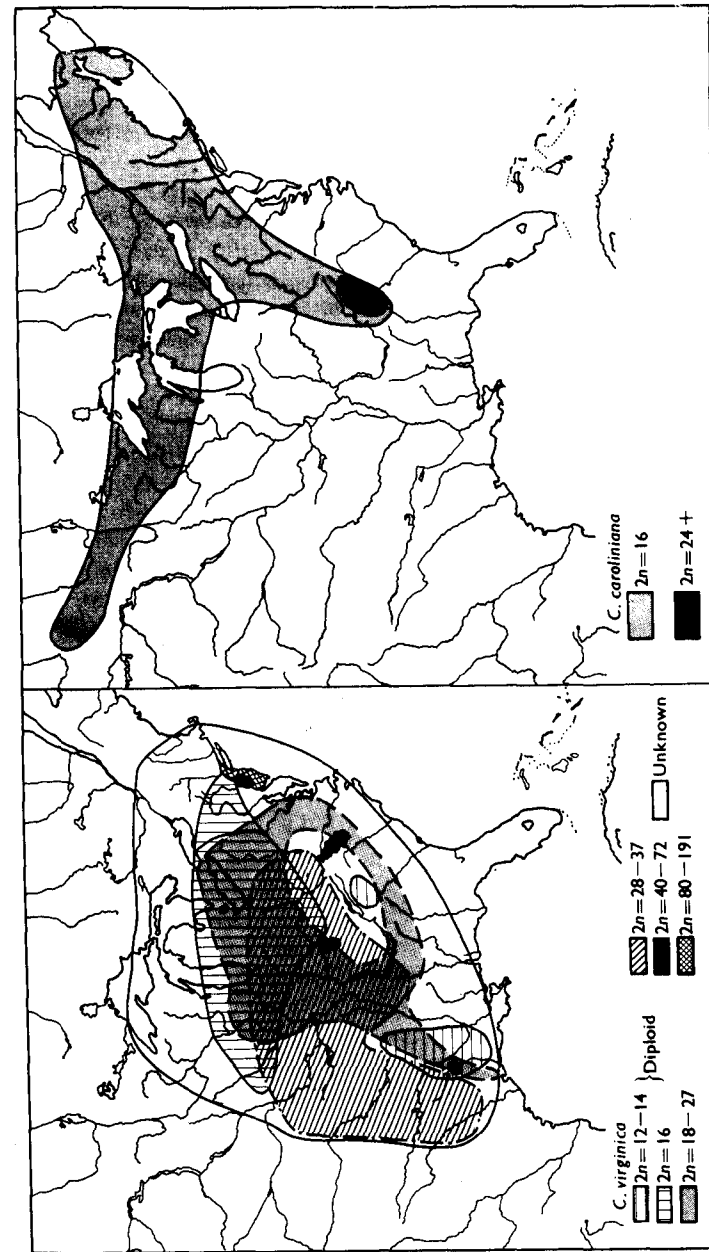


Fig. 6.8 Maps showing (a) the distribution of chromosomal races of *Claytonia virginica*, and (b) the generalized distribution of *C. caroliniana*. Note that diploids occur in three disjunct regions: the south-eastern Mississippi Valley ($2n = 14$); the southern Appalachian Mountains ($2n = 12, 14$), and probably through most of the northern half of the range of the species ($2n = 16$). The area of high chromosome numbers ($2n = 80-191$) may be more extensive than is indicated, since no counts are recorded from the regions to the north and east of New York City. (From Lewis, Oliver and Suda.¹⁴²)

degree of chromosomal duplication found among them, losses and gains of individual chromosome pairs would have less deleterious effects than in most other polyploid complexes.

Although the series found within the two taxonomic species, *C. caroliniana* and *C. virginica*, have been regarded as separate and independent 'autopolyploid' series, this supposition is not well supported by the morphological pattern of variation. The only visible differences between these species are in leaf width and the character of the inflorescence bract, the latter character being particularly unreliable. In respect to leaf width, a complete transitional series can be found in the southern part of their distributional areas.

The exact relationships within this complex will have to be clarified by hybridizations, particularly between the different diploids. Nevertheless, whatever may be the results of these experiments, *Claytonia* illustrates in a striking fashion the conservative influence of polyploidy. In spite of their very extensive chromosomal variation, these species are remarkably narrow in their overall range of morphological and ecological characteristics. All of their races are corm-forming inhabitants of deciduous woodlands in rich soil, which bloom in early spring and have a single pair of cauline leaves, a stereotyped architecture of their racemose inflorescences, and flowers, capsules and seeds which are very much alike. They represent multitudinous variations on a narrowly restricted theme.

The chronological age of mature polyploid complexes

Evidence from their distributional patterns indicates that most of the polyploid complexes which at present are in the mature state originated during the Pleistocene or Pliocene epochs, roughly between 500 000 and 10 000 000 years ago. In common with all evidence regarding problems of phylogeny, age and origin in groups without a fossil record, this evidence is indirect. Interpretations of modern distributional patterns are based upon the following assumptions, which are regarded as reasonable, in the light of ecological relationships between plants and their environment, and the migration of floras as indicated by the record of fossil pollens.

(1) Pleistocene and Pliocene distribution patterns were different from modern ones.

(2) During the Pleistocene epoch in North Temperate regions there were repeated oscillations of the flora southward and northward, in response to the oscillating climate.

(3) During the Pliocene epoch which preceded the glaciations, extensive mountain building activity in Eurasia, North America and South America disrupted previously continuous ranges, particularly of species adapted to mesic forest conditions.

(4) Since the development of initial and youthful polyploid complexes requires contacts and gene exchange between differently adapted diploids, the complexes which are now wide-spread and mature would have been able to acquire their present characteristics only if at an earlier time differently adapted diploids were sympatric and able to exchange genes with each other.

(5) New polyploids can extend their geographic distributions only if new habitats are opened up for them to colonize. Such events happened with particular frequency during the mountain building of the Pliocene and the retreat of glaciers during the Pleistocene.

Declining polyploid complexes

The decline of polyploid complexes first becomes evident through the existence of tetraploids or hexaploids which are not clearly related to any existing diploid. Although such situations might be explained on the assumption that the polyploids have diverged radically from their diploid ancestors by mutation and selection, the alternative explanation, that the diploid ancestor or ancestors have become extinct, is usually more compatible with other facts about the complexes concerned.

The decline of a polyploid complex is clearly evident in the Sections *Godetia* and *Biortis* of the genus *Clarkia*^{139,165,181} (Figs. 6.9 and 6.10). Among the nine species in these sections there are three diploids with $n = 9$, one with $n = 8$, two tetraploids with $n = 17$, and three hexaploids with $n = 26$. None of the diploids resembles the two tetraploids closely enough to be regarded as ancestral to them, and only *G. speciosa* gives evidence of relationship to the ancestors of the hexaploids. The age of the complex is further evident from the fact that of the two tetraploids one, *C. Davyi*, is restricted to the coast of California, while the other, *C. tenella*, is a highly diverse collection of races or ecotypes found throughout temperate Chile and in western Argentina, being the only species of *Clarkia* in South America.

In this complex, the clearest evidence of extinction is the close relationship between the hexaploid *G. purpurea*, which is wide-spread and common in California, and the tetraploid *G. tenella*, which is equally wide-spread and common in Chile. This relationship is evident both from morphological resemblance and from chromosome pairing in their F_1 hybrid. The former existence in California of a tetraploid similar to *G. tenella*, which was one of the ancestors of *G. purpurea* is, therefore, highly probable. One of the diploid ancestors of *C. tenella* and its extinct Californian relative was probably similar to the modern *C. speciosa* ($n = 9$), but the other ancestor, which presumably had 8 pairs of chromosomes, is apparently not represented by any modern species. The 9-paired species which combined with

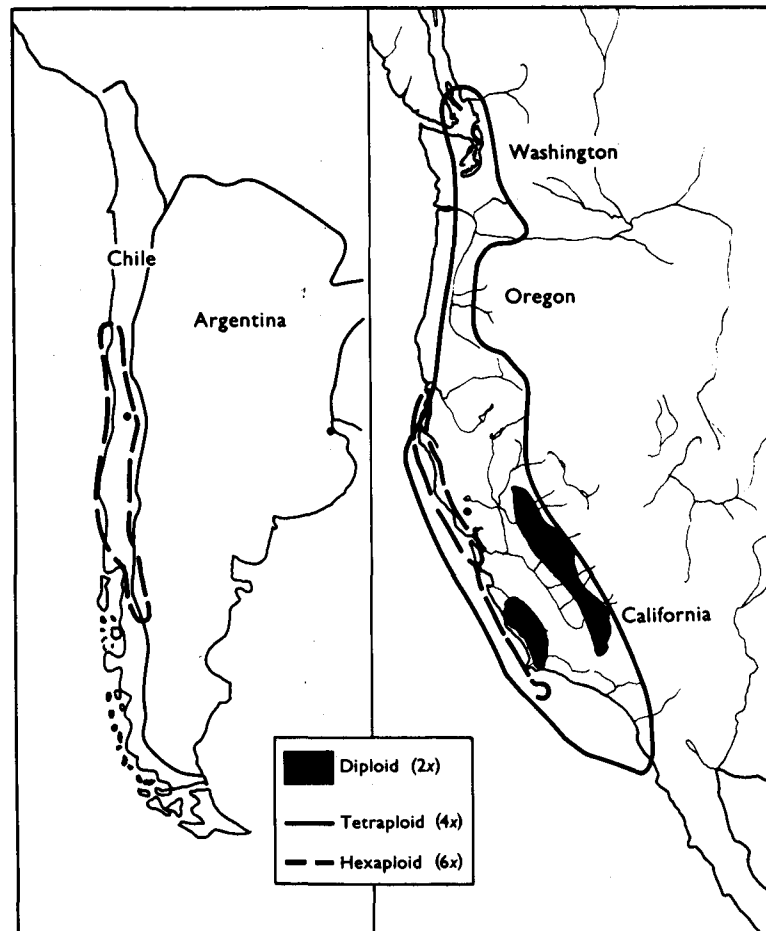
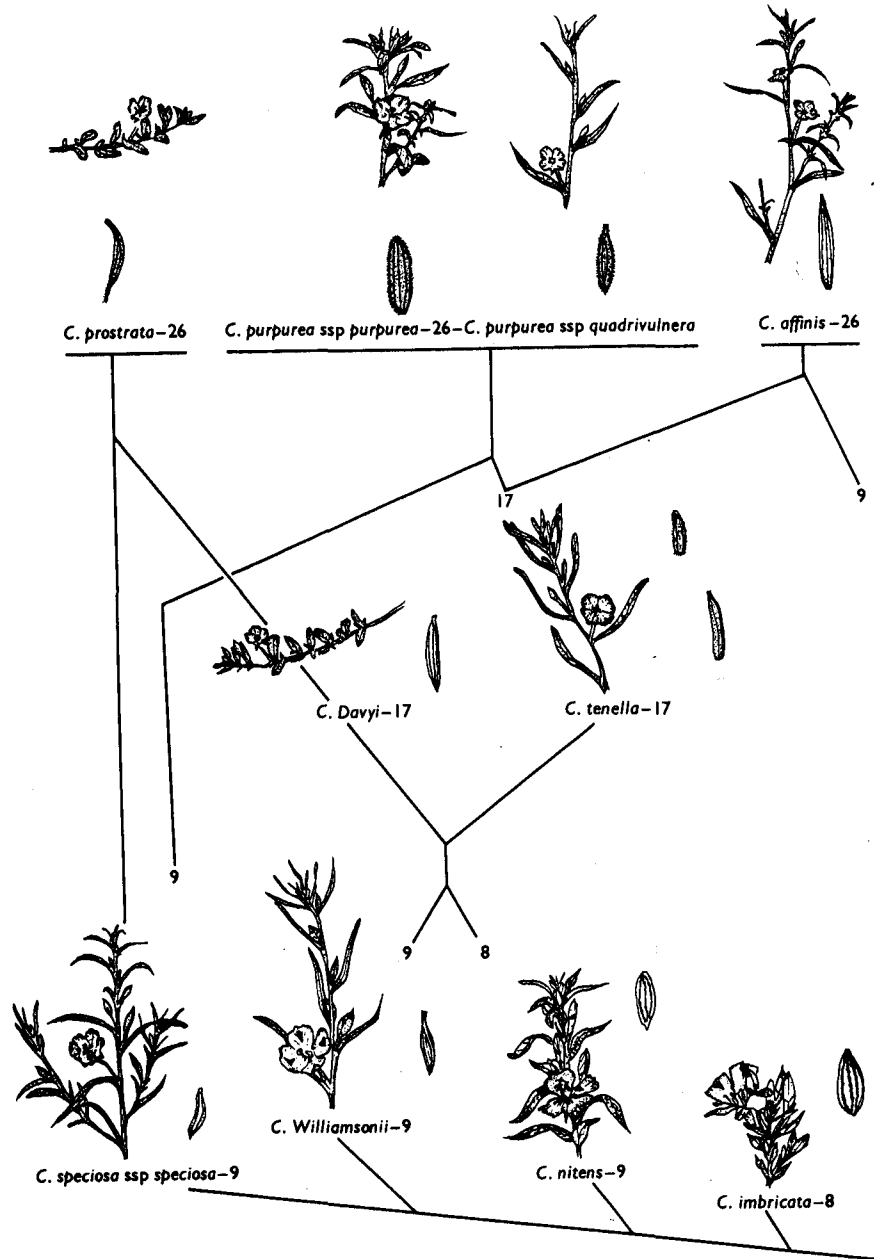


Fig. 6.10 (above) Limits of distribution of diploids, tetraploids, and hexaploids of *Clarkia* sect. *Godetia*. (From Lewis and Lewis.¹³⁹)

Fig. 6.9 (opposite) Representative plants and seed capsules of members of the polyploid complex of *Clarkia* subgenera *Godetia* and *Biortis*. The modern diploids all occur in California. The tetraploids ($n = 17$) are relatively rare in California but more common and much more variable in South America (Chile); the hexaploids are found throughout Pacific North America. At least one morphological characteristic, conspicuously pubescent capsules, occurs in the hexaploids and the South American *C. tenella*, but not in North American tetraploids or diploids. This suggests that a tetraploid or diploid possessing this characteristic, and ancestral to both *C. tenella* and the hexaploids, once existed in California but has become extinct. (From Lewis and Lewis.¹³⁹)



Fig. 6.11 Meiotic chromosomes (left); leafy branch with staminate cones and ovulate cone (middle) of modern *Sequoia sempervirens* ($2n = 66$); together with a leafy branch and an ovulate cone of the fossil *Sequoia* from the Oligocene Florissant Formation of Colorado. (Specimens from the collection of the Department of Paleontology, University of California, Berkeley).

the *tenella*-like tetraploid to give rise to *G. purpurea* is also probably extinct.

Relictual polyploids

The final stage of maturity of a polyploid complex is a high polyploid which has no close relatives. Several such examples are now known. One of them is the coast redwood of California, *Sequoia sempervirens*, which is a hexaploid ($2n = 66$). It is now regarded as a monotypic genus, since the other species previously assigned to *Sequoia*, '*S. gigantea*', is now recognized on the basis of many characters to belong to a different genus, *Sequoiadendron*. Although it is diploid, *S. giganteum* is probably not ancestral to *S. sempervirens*. There are a number of fossil redwoods which look much more like *S. sempervirens* but which have relatively smaller leaves and cones, suggesting that they may have been diploids (Fig. 6.11).

Several other endemic species of California have chromosome numbers which indicate a polyploid origin, but are nevertheless monotypic genera or ditypic. Among them are *Lyonothamnus floribundus* ($2n = 54$), *Dendromecon rigidum* ($2n = 56$), and *Simmondsia chinensis* ($2n = 52$). A relictual polyploid, wide-spread throughout the northern hemisphere, is *Brasenia Schreberi*, of the Nymphaeaceae ($2n = 80$).

THE RELATIONSHIP BETWEEN POLYPLOIDY AND APOMIXIS

Several polyploid complexes are characterized by *apomixis*, which is defined broadly as the replacement of sexual by asexual reproduction. Sometimes this replacement is through the presence of vegetative buds or leafy rosettes in positions where flowers would normally be expected, but more often seed production is involved. In *Citrus*, *Opuntia*, and a few other genera, apomictic seed production is made possible by *adventitious embryony*, or the production of embryos by budding of the nucellus or other somatic tissue of the seed. More commonly, however, apomixis is a two-step process. Through various modifications of meiosis in megasporogenesis which give rise to megaspores having the unreduced chromosome number, or through the formation of an embryo sac by a somatic cell of the nucellus or ovular integument, gametophytes and egg cells arise having diploid, unreduced chromosome number. Development may then continue without fertilization by *parthenogenetic* development of the egg cell, or by *pseudogamy*, which includes fertilization of the polar nucleus to form a hybrid endosperm, but development of the embryo from the egg cell without fertilization. The details of these processes can be found in other books.²⁰⁹

In some groups, such as the genus *Citrus* and a few species of *Potentilla*, apomixis has developed in diploid species or hybrids. Much more commonly, however, it is associated with polyploidy. As with sexual polyploids, the genetic constitution of apomictic polyploids forms a complete spectrum from strict 'autopolyploidy' to 'allopolyploid' origin resulting from crossing between widely different diploid parents. Furthermore, when groups containing apomictic polyploids are studied in their entirety, the entire spectrum is usually found within the same circle of relationship. Good examples are the American species of *Crepis* (Fig. 6.12), the subgenus *Eubatus* of *Rubus*, and the genera *Poa* and *Bothriochloa* of the grass family.^{27,53,208}

Secondary modification of apomictic complexes

Without full knowledge of the facts, one might expect that in polyploid complexes characterized by apomixis, secondary modifications would be less significant than in sexual complexes. This, however, is not the case, for several reasons.

Mutations of apomicts

In the first place, many apomicts are highly heterozygous genetically. This fact can be demonstrated by using the pollen of an apomict to fertilize a plant which is partly or entirely sexual. The resulting progeny

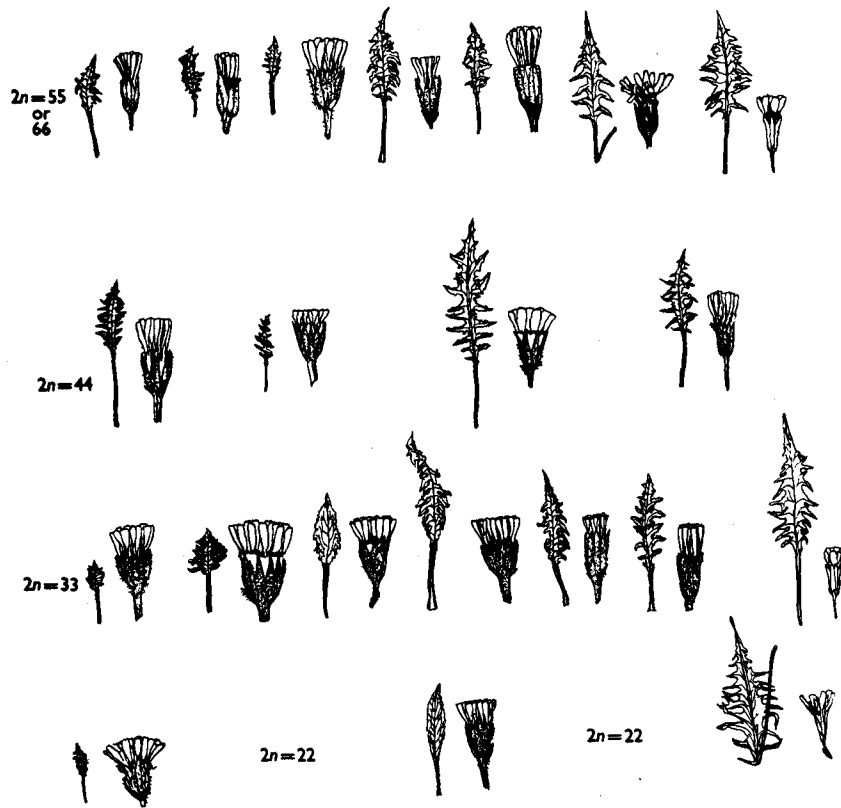


Fig. 6.12 Variability in leaves and capitula of a small sample of sexual species and apomicts of the *Crepis* apomictic complex in North America. Lower row, *C. modocensis* (left), *C. occidentalis* (centre) and *C. acuminata* (right): all diploid and sexual. Upper rows, apomicts showing various combinations of the characteristics of the three sexual species, and having somatic chromosome numbers of 33, 44, 55, and 66. (From Babcock and Stebbins.⁷)

are always highly variable.²⁰⁹ Because of this heterozygosity, many recessive as well as all dominant mutations alter the phenotype as soon as they appear. If, therefore, a single apomictic clone is propagated in large numbers for several generations, morphological variants always appear among its progeny.

Facultative apomixis

Secondly, many genotypes, known as *facultative apomicts*, are capable

of either sexual or apomictic reproduction. For any particular clone grown in a constant, defined environment, the proportion of sexual to apomictic seeds is fairly constant. It can be determined most easily in genera like *Potentilla*¹⁷² and some sections of *Poa*,³² in which pseudogamous fertilization of the endosperm is required for development, and which therefore produce functional pollen. Presumably, whether a particular ovule will produce a haploid egg that can be fertilized or a diploid egg that develops apomictically depends upon a delicate balance of opposing factors which operate during development.

This balance can be modified by altering the external environment. In the grass species *Dichanthium aristatum*, for instance, continuous exposure to short days results in a high incidence of apomixis (87–93%) while exposure to only the minimum number of short days required for flowering causes a much lower percentage (55–63%) of apomixis.^{124,125}

Geographic variations in the development of apomixis

In some groups, such as *Taraxacum*^{77,78} and *Dichanthium*,⁵³ the dominant form of reproduction varies in different parts of the geographic range of the same species. The races of *Taraxacum officinale* found in northern and western Europe are nearly all obligate apomicts. Most of them are triploids having completely inviable pollen, in which the growth of the embryo begins even before the flowers open. In central Europe, however, many diploid sexual races of *T. officinale* exist, and hybridization between this species and other *Taraxaca*, such as *T. laevigatum*, has been recorded.⁷⁷ Many new apomictic biotypes appear in the progeny of such hybrids, some of which can spread outward from their centre of origin. Probably, therefore, the great diversity of races or microspecies of *Taraxacum* found in western and northern Europe, as well as through introduction into North America, has resulted from successive migrations outward from the central European centre. Direct observations have shown that even within this centre, the apomicts show more aggressive, weedy tendencies than the sexual biotypes.

Some genera which contain many apomicts do not exhibit such clear-cut patterns. In some species groups of *Poa* and *Potentilla*, for example, facultative apomicts exist in greater or lesser proportions almost throughout the range of the complex, and centres of concentration for diploid, sexual races have not been identified.

Comparisons between sexual and apomictic polyploid complexes

In view of the radical difference between, on the one hand, sexuality and cross fertilization and, on the other hand, asexual reproduction via

apomixis, the similarity in both morphological variation pattern and eco-geographical distribution between sexual and apomictic polyploid complexes is striking. While young apomictic complexes have not yet been recognized as such, many mature complexes exist of which the diploids are relatively restricted in distribution and largely allopatric, while the polyploids are common, aggressive, and highly variable. The American species of *Crepis* (Fig. 6.13), and the genera *Taraxacum*, *Hieracium*, *Bothriochloa* and *Rubus* subg. *Eubatus* and *Antennaria* fit into this pattern. Furthermore, complexes like those of *Poa* and *Potentilla* resemble declining sexual complexes in that their diploid representatives are either extinct or hard to recognize as such, while higher levels of polyploidy in many areas predominate over tetraploidy. Finally one species *Houttuynia cordata*, which throughout its range is a high polyploid and is apomictic in all regions where it has been carefully examined,⁷ represents a relictual polyploid apomict.

The principal differences between sexual and apomictic polyploid complexes lie in the chromosome numbers represented and in the local variation patterns. Since irregular meiosis is no barrier to their seed formation, triploid, pentaploid and other odd-numbered apomictic clones can be as successful in polyploid complexes as can tetraploids, hexaploids, and octoploids. Interestingly enough, aneuploid clones are not formed in most apomictic complexes. Exceptions are those of *Poa alpina* and *P. pratensis*, in which an extensive aneuploid series has long been known.²⁰⁹

The presence of asexual reproduction by apomixis sometimes brings about extreme genetic constancy. This, however, is not the usual situation if entire populations are considered. More often, they consist of collections of apomictic biotypes, which have slightly different microhabitat preferences, so that they do not compete directly with each other. Figure 6.14 shows the kind of pattern that one finds if such a population is scored for two distinctive morphological characteristics. One can conclude from this figure that the population consists of two dominant apomictic biotypes, and four or five rare ones, represented by only one or two individuals. The pattern is much like the one obtained when a population of predominantly self-fertilizing species is similarly examined.

Because of the constancy of many apomictic races or 'microspecies,' some botanists have given them taxonomic recognition. The difficulty with this procedure lies only partly in the fact that by it the number of described 'species' becomes much too large. In addition, the method leads to absurdity if it is extended to cover the entire extent of any apomictic complex. This is because at least some populations contain facultative apomicts, which are continually crossing with each other to yield new clones. If these clones are regarded as species, then different offspring of the same parent must occasionally be placed in separate species.

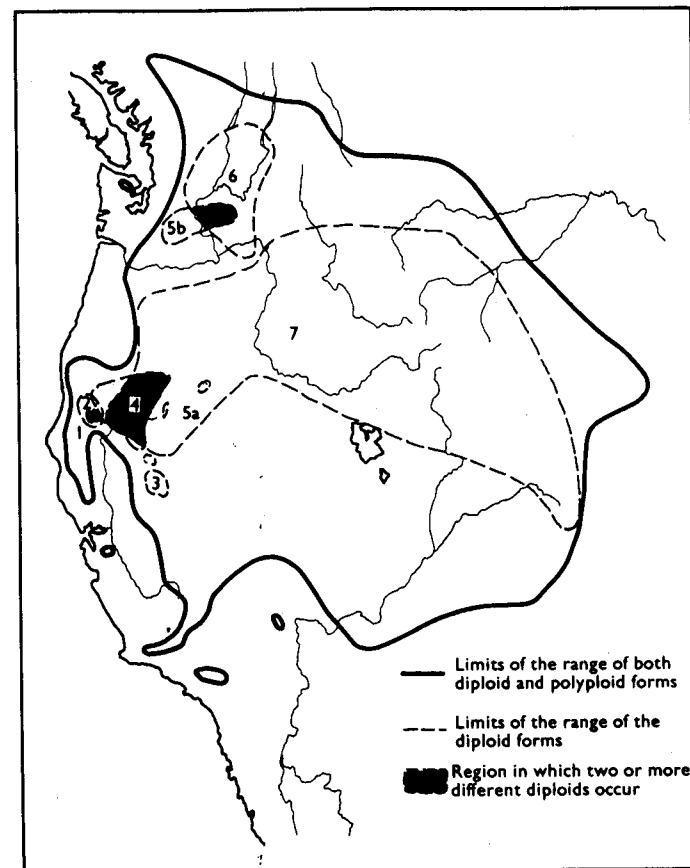


Fig. 6.13 Geographic distribution of the polyploid complex of *Crepis*. The three diploid sexual species illustrated in Figure 6.12 are nos. 3 (*C. occidentalis*), 5 (*C. modocensis*), and 7 (*C. acuminata*). (From Babcock and Stebbins.⁷)

The evolutionary future of apomictic complexes

Apomictic complexes have often been characterized as evolutionary 'blind alleys.' The viability of this statement depends upon what meaning is intended by it. There is no reason for believing that the acquisition of apomictic reproduction will either shorten the evolutionary life of a group of species or restrict its ability to colonize a large number of habitats. This is because all known apomictic complexes contain some sexual or facultatively apomictic populations, which from time to time enrich the

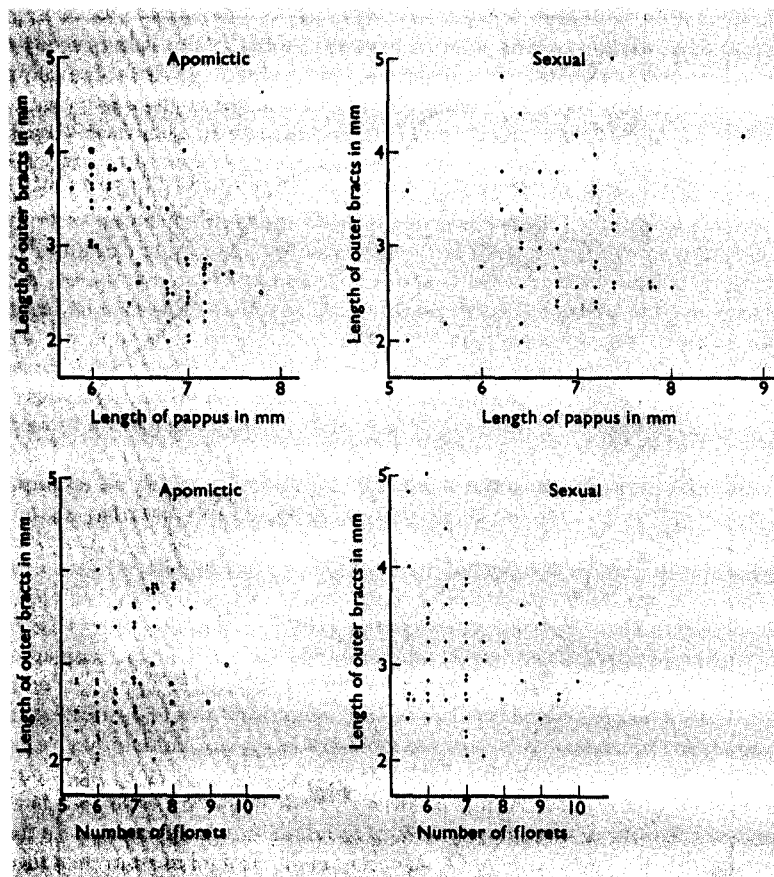


Fig. 6.14 Pattern of variability with respect to three morphological characteristics in an apomictic population of *Crepis acuminata* (left), as contrasted with a sexual population (right). In the upper scatter diagrams, length of outer involucre bracts (phyllaries) is compared with length of pappus; in the lower diagrams it is compared with number of florets. Note that the total range of variability in the apomictic population is less than that in the sexual population, but that the individuals of the former are grouped into two distinct clusters of variants. Individuals which on the basis of a combination of characteristics did not appear to belong to either of the two apomictic clones represented by the clusters are indicated by open circles. (From Babcock and Stebbins.⁷)

gene pool represented by the obligate apomicts.³¹ Distributional evidence suggests that some apomictic complexes are millions of years old. This is almost certainly true of the blackberries, *Rubus* subg. *Eubatus*, among which

exist groups of Old World apomicts that are related to those of the New World. This complex must have arisen and spread along with the Arcto-Tertiary flora during the Tertiary period. The apomictic complexes of tropical genera like *Panicum*, *Setaria*, and *Pennisetum* are likewise most probably of Tertiary origin, since tropical floras were probably not affected enough by Pleistocene changes in climate to afford opportunities for new polyploid apomicts to become established and spread. These complexes are now so wide-spread and successful in a variety of habitats that their extinction in the foreseeable future is hard to imagine.

On the other hand, the hypothesis that apomictic complexes will not give rise to new genera or families, or even to characteristics not present in their sexual diploid ancestors, is very plausible. The principal support for this hypothesis lies in the fact that all known apomictic complexes are contained within the same genetic comparium, in that their range of variation is bounded by a group of sexual or facultatively apomictic species which are capable of hybridizing and exchanging genes with each other. In certain large genera, such as *Poa* and *Hieracium*, the apomicts belonging to different subgenera have completely different mechanisms for circumventing meiosis. This suggests that in these genera apomixis has arisen more than once, and that their apomicts have not been able to extend their patterns of variation beyond the confines of a single section or subgenus. Most polyploid complexes, both sexual and apomictic, generate chiefly an endless number of variations upon a single adaptive theme. Nevertheless, some sexual complexes, through genetic diploidization and diversification of certain polyploids, have been able to break through the boundaries originally established by their diploid ancestors, and have given rise to new genera or even families. Once apomixis has set in, even this possibility is denied to the evolutionary line. It is doomed forever to generate one variant after another on the old, original theme. It will survive only as long as some of these variants are still adaptive in some habitat.

POLYPLOIDY AND PLANT DISTRIBUTION

There are three reasons why analyses of polyploid complexes can provide particularly valuable evidence for interpreting patterns of distribution in terms of past migrations of floras and origins of species. In the first place, the phylogenetic progression from lower to higher numbers, while not completely irreversible, is probably more so than is any other phylogenetic series which can be studied on the basis of modern forms. More important, in the case of young complexes as well as most mature ones, the phylogenetic progression can be duplicated in the laboratory and garden by artificial hybridization and chromosome doubling. Finally, in many

mature complexes the diploid representatives are now widely separated from each other, but polyploids exist which can be demonstrated experimentally to contain combinations of their chromosomes and genes. This is strong evidence in favour of the hypothesis that such diploids once occurred sympatrically with each other, so that they were able to hybridize and exchange genes. By putting this evidence together with that derived from fossil floras which indicate the past distribution of certain kinds of plant communities, a synthesis can often be achieved which sheds much light upon past migrations and alterations of floras. In order to do this, we must consider the relationship of polyploids to climatic, edaphic, and historical factors.

Polyploidy and climate

Early studies of the geographic significance of polyploidy emphasized its relationship to major climatic differences. The hypothesis was advanced that polyploids are better adapted than their diploid progenitors to extreme cold and drought. The difficulties with this hypothesis have already been pointed out by several authors.²⁰⁹ The data regarding cold resistance were obtained chiefly from Europe, where percentages of polyploidy in the flora as a whole definitely increase as one goes northward to higher latitudes. On the other hand, the percentage of polyploids in the flora of the high Alps, comprising the rocky refuges for plants which exist above the snow line, is no higher than in the plains and foothills below.⁶⁹

The hypothesis that desert regions contain high percentages of polyploids was based upon a few examples taken from the flora of Timbuktu. More recent studies of the floras of arid zones fail to confirm this hypothesis. Particularly enlightening are comparisons of the distribution of diploid and polyploid populations belonging to groups which are distributed both in desert regions and in the more mesic regions adjacent to them. Such comparisons, which are summarized for western North America in Table 6.2, give no support to the hypothesis that polyploids are in general more tolerant of drought than their diploid ancestors. Furthermore, physiological comparisons of artificial autopolyploids with their diploid progenitors have shown that such polyploids have a decreased resistance to drought.²⁰⁹

The hypothesis that equable climates favour diploids and extreme climates favour polyploids has been finally made untenable by the results of cytological investigations of tropical rain forest floras, particularly that of the Ivory Coast,¹⁵⁴ the fern flora of Ceylon,¹⁵⁷ and certain families (Labiatae, Commelinaceae) in West Africa^{166,167} and India.¹⁸⁰ If genera having high basic numbers are regarded as originally polyploid, the

Table 6.2 Comparison between pairs of diploid and closely related polyploid races or species, one or both of which are found in desert or steppe regions of the western United States. In only one out of nine examples is the tetraploid found in more xeric habitats than its diploid relatives.

Genus and Reference	Diploid	Ecological occurrence	Polyploid	Ecological occurrence	Comparison polyp/2x
<i>Ambrosia</i> , Payne et al. ¹⁷⁶	<i>A. deltoidea</i>	Deserts	<i>A. chenopodiifolia</i>	Dry hills, coastal	More mesic
<i>Artemisia</i> , Ward ²³⁷	<i>A. tridentata, cana, arbuscula</i>	Dry open steppes	Same, plus <i>A. Rothrockii</i>	Dry open steppes or dry forests	Similar or more mesic
<i>Castilleja</i> , Heckard ⁶⁹	<i>C. chromosa</i>	Dry open steppes	Same, plus <i>C. affinis</i>	Steppes, chaparral, forests	Similar or more mesic
<i>Dudleya</i> , Uhl and Moran ²³⁴	<i>D. Abramsii</i> <i>D. saxosa aloides</i>	Deserts, desert margins	<i>D. lanceolata</i> <i>D. saxosa saxosa</i>	Desert margins, coastal chaparral	Similar or more mesic
<i>Eriogonum</i> , Stebbins ²⁰⁸	<i>E. fasciculatum</i> <i>ssp. polifolium</i>	Deserts, desert margins	<i>E. fasciculatum</i> <i>ssp. foliosum</i>	Chaparral, interior and coastal	More mesic
<i>Galium</i> , Dempster and Ehrendorfer ⁵⁰	<i>G. Mathewsii</i> , <i>magnifolium</i> , <i>multiflorum</i> , <i>coloradoense</i>	Desert margins, dry forests	<i>G. argense, Munzii, hilendae</i>	Desert margins, dry forests	Similar
<i>Gutierrezia</i> , Solbrig ²⁰¹	<i>G. microcephala</i>	Deserts	<i>G. bracteata, californica</i>	Desert margins, chaparral	More mesic
<i>Haplopappus</i> , Raven et al. ¹⁸²	<i>H. acradenius</i> ssp. <i>bracteosus</i>	Semi-arid valleys	<i>H. a. acradenius</i>	Deserts	More xeric
<i>Sidaicea</i> , Hitchcock and Kruckeberg ¹⁰⁴	<i>S. multifida</i>	Open steppes	<i>S. glaucescens</i>	Dry forests	More mesic

percentage of polyploidy in these floras ranges from 85 to 95 per cent. Present data suggest that the lowest percentages of polyploidy are found in floras of warm temperate and subtropical regions, and that percentages increase as we go from these regions either toward the cooler or the tropical areas.

Edaphic and historical factors affecting the distribution of polyploids

More significant than the correlations with climate are correlations with degree of disturbance as well as with the age of habitats. In compiling the data for such correlations, one cannot deal with floras as wholes, because of the great differences in the frequency of polyploidy in plants having different life cycles and growth habits and particularly because the proportion of plants having different life cycles and growth habits differs greatly from one habitat to another. In particular, many habitats which have been recently opened up by human activity, such as old fields and roadsides, contain unusually high proportions of annual species, among which polyploids are much less frequent than among perennial herbs (Table 5.1). Consequently, the fact that in Canada the percentage of polyploids among weeds is the same as in the flora as a whole¹⁷⁰ does not tell us anything about the relative probability of becoming weedy among related diploids and polyploids which have the same growth habit. Significant facts about the distribution of polyploids are much more likely to be obtained from comparisons within groups of related species and chromosomal races than from statistical comparisons of entire floras. The results of representative intra-group comparisons will be given for plants having various habits of growth and occupying areas which have been subjected to various kinds of disturbances.

Annual weeds of fields and roadsides

The most reliable data on these plants can be obtained in the case of species groups which are native to regions recently opened to cultivation, and have therefore acquired their weediness in modern times. Seventeen such groups exist in the California flora, and among them there are 36 species which have become weedy. Of these 15, or 42 per cent, are polyploid, which compares with a figure of 31 per cent polyploidy for the flora of California as a whole, and 17 to 20 per cent for species of annuals with known chromosome numbers. Thirteen of these species have diploid non-weedy relatives in California, one (*Bromus arizonicus*, see p. 133) is a high polyploid having ancestors with lower degrees of polyploidy elsewhere in America, and the remaining tetraploid species (*Calandrinia ciliata* var. *Menziesii*) has Californian relatives of which chromosome numbers are not

known. A nearly complete list of these species is given elsewhere.²¹⁵ None of the diploid annual Californian weeds has polyploid relatives which are not weedy.

These data lead to the conclusion that diploid annuals belonging to genera not containing polyploid annuals have a good chance of becoming weedy, but that if related diploids and polyploids exist in the same group of annuals, the polyploids have a greater chance of becoming wide-spread as weeds than their diploid relatives. This conclusion is supported by the distribution pattern of the genus *Aegilops*, which has already been described (Fig. 6.3).

Polyploidy and edaphic factors

The bearing of edaphic factors on the relative distribution of diploids and polyploids has received far less attention than it deserves. The immediate availability of habitats for colonization by newly formed polyploids depends much more upon such factors as the nature of the soil, local differences in temperature, and the density and character of existing vegetation than it does upon the overall climate. Hence we need to know much more than we do about the relative frequency of polyploids in different habitats within the same climatic zone.

The promising results which can emerge from such studies are well illustrated by Johnson and Packer's analysis¹¹⁴ of the Ogotoruk Creek Flora of northwestern Alaska. In this arctic flora, from 68° north latitude, an environment gradient scale was established on the basis of soil characteristics. When the frequency of polyploids was compared between plant communities occupying different positions on this scale, the highest frequency (88%) was found in lowlands having fine textured soils with high moisture, low temperature, shallow permafrost and high disturbance (Fig. 6.15). At the other end of the scale the communities occupying soil having coarse texture, low soil moisture, high soil temperature, deep permafrost and low disturbance had only half as many polyploids (43%). Since in this arctic climate annuals as well as trees are virtually absent, the communities examined were sufficiently similar in respect to the life forms represented that variations due to this factor could not have affected the results.

Similar data need to be obtained on floras of other regions. Even more significant data could be obtained by confining the observations to those genera having different levels of ploidy in the same geographic region.

Polyploidy and glaciation

The observations of Johnson and Packer were made in order to provide information regarding the effects on the frequency of polyploidy in the

North Temperate Zone of the Pleistocene glaciations themselves as well as of associated disturbances which occurred in surrounding unglaciated regions. Although the Ogotoruk Creek area was itself not glaciated, its habitats certainly suffered great changes during the Pleistocene, the magnitude of the changes having been greatest with respect to the communities at the left hand end of the scale in Figure 6.15. The results of this study, therefore, support the conclusions that polyploids are at a selective advantage in habitats which have been subjected to frequent and drastic fluctuations in both climate and edaphic factors.

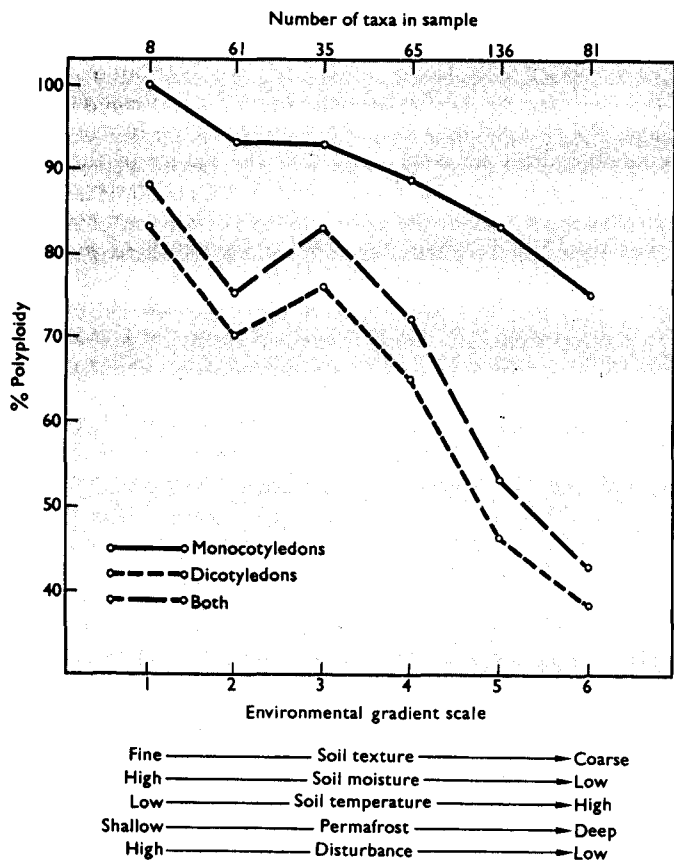


Fig. 6.15 The relationship of the frequency of polyploids in the angiosperm flora of the Ogotoruk Creek Valley, Alaska, to environmental gradients of soil character, moisture, and persistence of frost. (From Johnson and Packer.¹¹⁴)

The mistaken notion that polyploidy has evolved in response to increasingly cold climates arose because the first comparative data made available were those obtained from western Europe and the islands to the north of this continent. In these regions, three different factors vary with increasing latitude to the same degree and in the same places. These are increasing cold, increasing effects of glaciation (except possibly for a few relatively small nunatak areas), and increasing isolation due to insularity. Along the Pacific Coast of North America, these factors are separated from each other. Insularity need not be considered, since such islands as exist are so close to the continent that seed dispersal to them presents no problem. The severity of climate along this coast increases most drastically between 53° and 68° north latitude. At 53° (Queen Charlotte Islands), the mean temperature for the coldest month is about 0°C, and the abundant moisture supports a luxuriant forest, at lower altitudes. At 68° (north-western Alaska), winter temperatures reach -40°C, and permafrost extends to depths of over 300 m. On the other hand, the effects of glaciation are already strong at 53°, and are little, if any, stronger at 68°, since this region of north-western Alaska was largely unglaciated. The major difference between regions little affected and those much altered by the glaciers themselves as well as by their influence upon surrounding territories occurs between 40° and 50° north latitude.

Estimated percentages of polyploidy in the Pacific Coast flora of North America are 36 per cent for northern coastal California at about 40°, 53 per cent for the Queen Charlotte Islands at 53°²²⁹ and 56 to 59 per cent for north-western Alaska at 68°.¹¹⁴ These data show that the maximum increase in percentage of polyploidy is associated not with the maximal change in climate, but with the greatest difference with respect to the effects of glaciation.

Further information on the relationship of polyploidy to glaciation can be obtained by comparing the distribution of diploids and polyploids belonging to individual complexes with the extent of glaciation in the regions where they occur. That of *Biscutella laevigata* and its relatives in the Alps and the surrounding mountains is particularly instructive (Fig. 6.16). Diploid races or subspecies have persisted in montane refuges both to the west and the east of the major glaciated area of the central Alps, the latter being occupied almost entirely by tetraploid populations. These surrounding unglaciated or little glaciated mountains are refuges for diploids in many other groups which have contributed polyploids to the flora of the glaciated area.^{65,70} In North America, the distribution of *Iris versicolor* ($2n = 108$) and its probable diploid ancestors, *I. virginica* var. *Shrevei* and *I. setosa* var. *interior* (Fig. 6.17), is equally instructive.

To produce situations like these, the following sequence of events probably took place. Before any particular advance of an ice sheet, the worsening climate opened up habitats for the hardier members of the

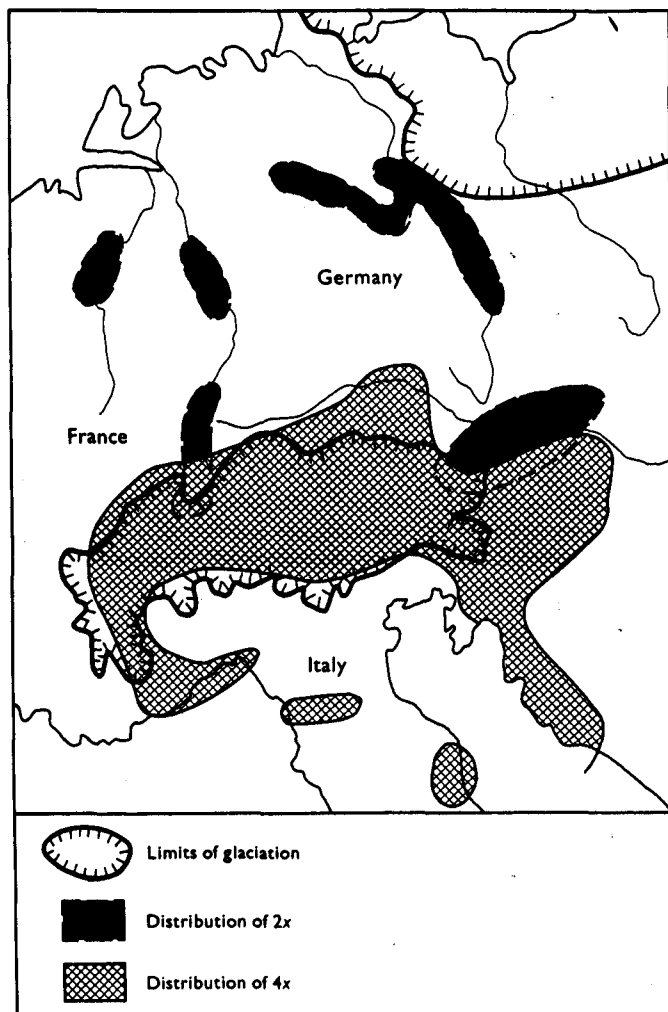


Fig. 6.16 The association between the distribution of diploid and tetraploid *Biscutella laevigata* and the Pleistocene glaciation of Central and Northern Europe. The diploids occur chiefly in unglaciated river valleys between regions covered by the northern and the alpine glaciers. The tetraploids occur throughout the area covered by the alpine ice sheet, and extend from there southward and eastward. (From Manton,¹⁵⁵)

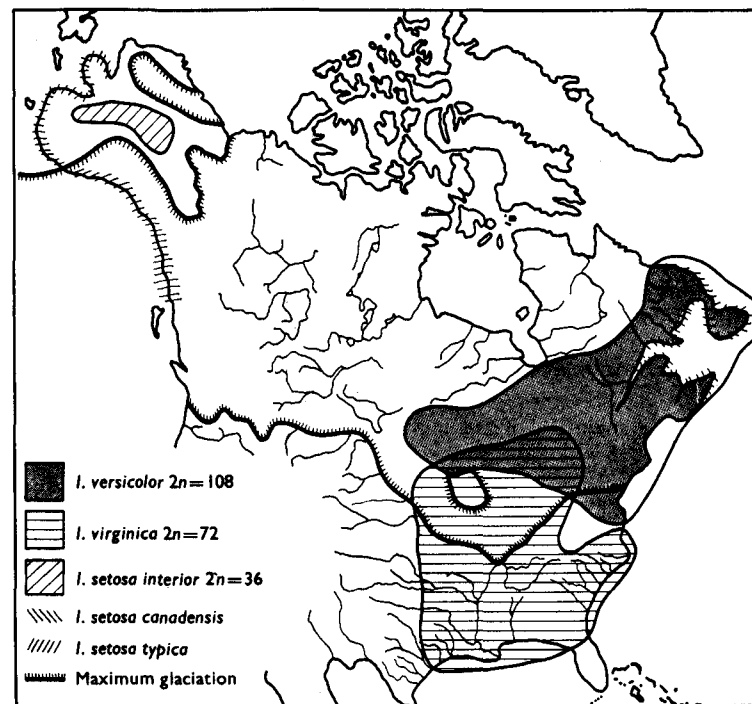


Fig. 6.17 The distribution of the hybrid polyploid *Iris versicolor* and its probable ancestors in relation to the Pleistocene glaciation of North America. The distribution of *I. versicolor* is almost entirely within glaciated territory; *I. virginica* is in both glaciated and unglaciated regions; *I. setosa* var. *interior* occurs in the unglaciated regions of central Alaska. Its former occurrence along the southern margin of the ice sheet in eastern North America is postulated. (Data of E. Anderson, from Stebbins,²⁰⁹)

group, through destruction of the less hardy members of the pre-existing vegetation. In a mountainous region, this destruction would have varied greatly according to slope, insolation, and the character of the soil. Consequently, differently adapted populations would have in many places become established near each other, and hybridization between them would have been possible. With the formation and advance of the glaciers themselves, these variably distributed conditions would have become general around the margins of the ice sheet, and would have persisted throughout the glacial period. Consequently, many hybrids as well as polyploids having various degrees of hybrid origin probably existed around these margins when the retreat of the ice began. Geological evidence indicates that in

both montane and flat areas this retreat was highly irregular, so that in many places adjacent areas would have supported on the better and warmer soils the beginnings of forest associations, and on the poorer, colder soils the remnants of the retreating tundra vegetation. These conditions would have provided more opportunities for hybridization between diploids, between different ones of the newly formed polyploids, and between polyploids and their diploid ancestors. From these rich, variable gene pools the genotypes best adapted to the habitats being opened up by the retreating ice would have become established and spread by natural selection. Most of these were polyploids, but in some groups diploids also became adapted to these new conditions.

Effects on polyploidy of pre-glacial environmental changes

By far the majority of the polyploids of which the ancestry can be determined with any degree of certainty have distribution patterns which suggest an origin during the Pleistocene or recent epochs, or perhaps during the end of the Pliocene epoch, when the climate was deteriorating prior to the advance of the ice sheet. This is true of virtually all of the analysable polyploid complexes of California, which have been listed elsewhere²²⁰ as containing 'patroendemics' or 'apoendemics'. Nevertheless, many polyploids have distributional ranges which cannot easily be explained on this basis. This is particularly true of polyploids which are native to temperate or warm regions of both the Old and New World, as well as of those which are confined to one continent, but have at least one ancestor now existing only on another continent. Several polyploid species of ferns are known from both Eurasia and North America, of which *Asplenium trichomanes* is a good example. Among seed plants, the hexaploid race of the grass *Heteropogon contortus*, found in subtropical Africa, Asia and North America, and tetraploid *Themeda quadrivalvis*, found in Africa, Asia and Australia, are both good examples. These species must have acquired their distributional ranges at a time when migrations from one continent to another were accomplished more easily than they are at present.

The same is true of examples such as the species of *Lactuca* and *Crepis* endemic to North America.^{7,42} Those of *Lactuca* all have the gametic number $x = 17$, and have relatives in Asia with $x = 8$ and $x = 9$. The American species of *Crepis*, which form a polyploid series based upon $x = 11$, probably originated as hybrid polyploids between different Asiatic species having $x = 4$ and $x = 7$. Throughout the Pleistocene and recent epochs the climates of the Siberian-Alaskan land bridge which connects Asia with America have been arctic or subarctic, and too inhospitable for these temperate plants. However, evidence from fossil pollen indicates that this land bridge could have been suitable for them

during the middle of the Tertiary period, when these polyploids probably arose. This hypothesis is compatible with the amount of diversification found in these two species groups, which can then be explained in relation to changes in the flora which took place during the latter part of the Pliocene as well as the Pleistocene epoch.

The principal kinds of environmental changes which took place during most of the Tertiary period and in some parts of the world during the Cretaceous period, and could have provided conditions favourable for the origin and spread of polyploids, were the following. Extensive mountain building brought into existence many new alpine and subalpine habitats.⁵ At the same time, this activity produced many 'rain shadow' areas in the interior parts of the continents, which consequently became much drier, and developed continental climates having extreme seasonal differences in temperature. In addition, the Cretaceous and Tertiary periods witnessed a succession of evolutionary appearances of new kinds of grazing animals. Grazing dinosaurs, large flightless birds (Ratitae), primitive ungulates, Titanotheres, elephants, horses, camels, antelopes, sheep and bovinds all arose at various times. Both by their different methods of grazing and browsing, and the different degrees to which they trampled the soil, they must have created new and sometimes drastic pressures upon the existing vegetation. Moreover, these animals must have often transported seeds from one region to another in their hair or in the mud adhering to their legs and feet. The catastrophic effects which are exerted on vegetation by the introduction of new grazing or browsing animals that carry with them the seeds of new kinds of plants are evident both from the almost complete replacement of native herbs by introductions from Eurasia during historical times in America and Australia, and from the damage which the forests of Hawaii and other Pacific islands have suffered, and those of New Zealand are still suffering, from similar invasions. Although the association of individual appearances of polyploidy in particular groups with specific examples of these changes may never become possible, we must be aware of the fact that they have been taking place in various places from time to time throughout the evolutionary history of the flowering plants. We can thus expect to find polyploid complexes of various ages, a conclusion which has already been reached on the basis of comparisons between the distributional patterns of individual complexes.

Polyploidy and endemism

A subject which has always been of great interest to plant geographers is the occurrence of endemic species restricted to narrowly confined areas of distribution. Although in the past great controversies have arisen between some botanists who thought that all endemics are of recent origin