POLYPLOIDY, HYBRIDIZATION, AND THE INVASION OF NEW HABITATS

G. LEDYARD STEBBINS[1]

ABSTRACT

Experiments are described showing that most artificial autopolyploids derived from native or introduced perennial grass species from California are far inferior in behavior under field conditions than their diploid ancestors. In a single species, *Ehrharta erecta* in two out of 22 localities, the autotetraploid maintained itself for, respectively, 19 and 39 years, but remained either in the exact locality of planting or in nearby localities having very similar ecological conditions. The control diploids, direct descendants of the progenitors of the autopolyploids, spread more widely and evolved more variation with respect to growth habit among each progeny. These results, along with other evidence derived from several literature sources, strengthen the hypothesis that successful polyploids among natural populations are usually or almost always the result of increased heterozygosity accompanying either interracial or interspecific hybridization. The hypothesis that polyploids succeed because of their greater tolerance of severe ecological or climatic conditions is again rejected, and that which postulates secondary contacts between previously isolated populations as the principal cause for their high frequencies in some groups of angiosperms is favored. The unusually high frequency of polyploids in the Gramineae is attributed to the probable fact that habitats to which they are best adapted have changed in extent and position repeatedly during the geological periods since the initial evolution of the family.

The family Gramineae contains higher percentages of species and races or cytotypes of polyploid origin than any other large family of angiosperms. More than 80% of its species have undergone polyploidy some time during their evolutionary history. Polyploidy is expressed by four different kinds of numerical series, as follows:

(1) Multiples of an original low basic number. Examples: *Triticum, Bromus,* and *Festuca* that include species having somatic numbers of $2n = 14, 28, 42, \ldots$, basic number $x = 7$.

(2) Multiples of a secondary basic number, that was itself derived from the original number by an earlier cycle of polyploidy. Examples: *Poa scabrella* complex, $2n = 42, 84$, $x = 21$ (Hartung, 1946); *Bothriochloa saccharoides* complex, $2n = 60, 120, 180$, $x = 30$ (Gould, 1966); and Australian species of *Danthonia*, $2n = 24, 48, 72$, $x = 12$ (Brock & Brown, 1961).

(3) Multiples of a basic number that is the lowest in its genus, but was probably derived from that of preexisting genera by a cycle of polyploidy in the remote past. Examples: *Oryza*, $2n = 24, 48$, $x = 12$ and *Tripsacum*, $2n = 36, 72$, $x = 18$ (Fedorov, 1969).

(4) Aneuploid series that most probably represent successions of alloploids based upon different basic numbers. Example: *Stipa*, $2n = 22, 24, 28, 32, 34, 36, \ldots 82$. All of the numbers listed in Fedorov (1969) can be derived from various combinations of the basic gametic numbers $x = 5, 6$, and 7.

The existence of these four kinds of situations indicates that polyploids in this family include, in addition to those that have originated recently during the past few thousand years, other polyploids that are intermediate in age from one to several million years and still other genera that acquired a secondary polyploid number during the early evolution of the family 50–70 million years ago. The original basic number for the family has been the subject of much speculation, but no convincing evidence has been presented for any of the various hypotheses. In this writer's opinion, the basic numbers $x = 5, 6$, and 7 are almost equally probable. They could, in fact, have all been acquired by the species complex from which the family first arose. Moreover, the presence of $x = 11$ in *Streptochaeta*, a genus that is very much isolated with respect to morphological characters, and at the same time is a mosaic of very primitive characteristics along with others that are highly specialized, suggests that polyploidy, along with trends toward aneuploidy and a high degree of specialization with respect to some morphological characteristics, evolved quickly and soon after the family first became differentiated. Accordingly, the early stages of grass evolution must have produced many species

---

[1] Department of Genetics, University of California, Davis, California 95616.

ANN. MISSOURI BOT. GARD. 72: 824–832. 1985.

and genera that are now completely extinct. Hence in the absence of diagnostic fossils, any attempt to reconstruct the early evolution of grasses, including the first occurrences of polyploidy must be regarded as futile and self-defeating.

Another distinctive feature of the Gramineae is that the high frequency of polyploidy prevails throughout the family. Nearly all of the other large families of angiosperms: Liliaceae, Orchidaceae, Ranunculaceae, Rosaceae, Leguminosae, Onagraceae, Umbelliferae, Scrophulariaceae, Rubiaceae, and Compositae, include a few large genera in which polyploids are a minority of species or are totally absent. Not so in the Gramineae: its largest genus in which the majority of species are diploids is *Melica*, containing about 60 species; a modest number compared to such giants as *Festuca* (150 spp.), *Panicum* (500 spp.), and *Paspalum* (200 spp.). Because of this situation, Gramineae are not well fitted for making comparisons between related genera that differ greatly from each other with respect to the frequency of polyploidy. Hence in discussing reasons for high frequencies of polyploidy, I shall make comparisons between genera belonging to other families.

CURRENT HYPOTHESES TO EXPLAIN HIGH FREQUENCIES OF POLYPLOIDY

During the past 60 years, several hypotheses have been advanced to explain different frequencies of polyploidy in a given flora or group of plants. The principal ones are: (1) Many polyploids are more resistant to extreme temperatures, either cold or heat, than their diploid relatives. (2) Polyploids include a higher proportion of drought resistance genotypes than do related diploids. (3) Polyploids are better adapted than their diploid relatives to invasion of new habitats. None of these is entirely satisfactory.

The hypothesis of greater cold resistance, first proposed by Tischler (1935) and more recently supported by Löve and Löve (1949) and others, has been severely criticized by Favarger (1957), Gustafsson (1948), and the present writer (Stebbins, 1950). It is contradicted by most experimental autopolyploids, which are less resistant to frost than are their diploid progenitors. If it were the major reason for high frequencies of polyploidy in Gramineae, we would expect to find higher frequencies of polyploidy in temperate and arctic genera than in tropical genera. As is evident from the high degree of polyploidy in such tropical genera as *Paspalum, Saccharum,* and various genera of Bambuseae, this is not the case. The same criticisms can be raised against the hypothesis that polyploidy has become generally and significantly more prevalent because of present or past exposure to severe drought. With respect to drought, in fact, some examples of increasing polyploidy have been associated with adaptation to more mesic habitats on the part of the higher polyploids. This is true of hexaploid as compared to tetraploid varieties of wheat, tetraploid as compared to ancestral diploid species of perennial Triticeae such as *Elymus* (*Psathyrostachys*) *junceus* (Dewey, 1970), and polyploid as compared to diploid species of *Bouteloua* (Gould, 1966; Stebbins, 1975).

Hence one can safely conclude that greater resistance to cold or drought is not produced by polyploidy or chromosome doubling per se. In some instances, a polyploid cytotype may be more resistant than one of its diploid relatives, but this is probably due to the acquisition of greater resistance from another source, either mutation or, more probably, hybridization.

With respect to both of these hypotheses, a relevant set of data is the geographical and ecological distribution of the 12 species having the highest number of chromosomes known in the family. These are listed in Table 1. They encompass a wide range of taxonomic diversity, including eight tribes (Agrosteae, Andropogoneae, Aveneae, Chlorideae, Danthonieae, Eragrosteae, Festuceae, and Paniceae) and four subfamilies (Arundinoideae, Eragrostoideae, Panicoideae, and Pooideae), thus emphasizing the wide distribution of high polyploidy in the family. Their geographic distribution is equally diverse. They grow in a variety of climatic zones and habitats, from tropical to polar and desert margins, although the largest single category of habitats is cool or warm temperate, and insular, with relatively little seasonal fluctuation in temperature. These data support many others in pointing toward the lack of correlation between distribution of polyploids and any particular kind of habitat or geographic region. The principal reasons for the high frequency of polyploids in grasses must be sought among factors other than edaphic-physiological or geographic.

The only hypothesis that emphasizes other factors is that which postulates greater ability of polyploids to invade and colonize new or disturbed habitats than that of their diploid progenitors. This hypothesis assumes that poly-

TABLE 1. Twelve species of Gramineae having the highest levels of polyploidy.

Species	Somatic Number	Basic Number	Ploidy Level	Geographic Distribution
Alopecurus alpinus	130	7	18–20*x*	Circumpolar
Andropogon (*Bothriochloa*) *barbinodis*	180	10	18*x*	SW United States, Mexico
Calamagrostis crassiglumis	140	7	20*x*	Pacific North America
Ctenium concinnum	160	10	16*x*	South Africa
Danthonia induta	120	6	20*x*	Southwestern Australia
Dupontia Fisheri	132	11	12*x*	Arctic
Echinochloa stagnina	126	9	14*x*	Assam, India
Helictotrichon (*Avena*) *pratense*	126	7	18*x*	Britain, Scandinavia
Poa litorosa	263–265	7	38*x*	Auckland Islands, New Zealand
Poa rigens	127	7	18*x*	Iceland
Saccharum robustum	194	10	18–20*x*	New Guinea
Sporobolus airoides	126	9	14*x*	SW United States

ploids can arise and maintain themselves in a variety of habitats, depending upon their genetic constitution, but only those having an unusually strong capacity for colonization will become widespread. It was advanced by Reese (1958) as an alternative explanation for the high frequency of polyploids in the flora of northern Europe and has been supported by the present author (Stebbins, 1972), Darlington (1973), and Ehrendorfer (1980). It is, however, incomplete. It simply raises another question: How do successful, widespread polyploids acquire their greater capacity for colonization? The following sections of this contribution will be devoted to a discussion of this problem.

ARTIFICIAL TETRAPLOID *EHRHARTA ERECTA*: A LONG TERM FIELD EXPERIMENT

The most direct evidence that can be obtained on the possible effect of polyploidy in increasing evolutionary success consists of field experiments in which polyploids and their known diploid ancestors are planted simultaneously in the same area and their relative success is compared. With respect to strict autopolyploids of non-hybrid origin, the one that I have conducted during 39 years on a South African species, *Ehrharta erecta*, which became established as an adventive in northern California about 1930, is the most extensive and long lasting that is known to me. As stated in the account published with the record of the first few years of this experiment (Stebbins, 1949), it was begun after screening colchicine induced polyploids belonging to 20 species and nine genera of grasses, the diploid progenitors of which all are well adapted to persistence in the natural vegetation of northern California. Of these species, only *E. erecta* survived the preliminary screening and was judged worthy of comparing the artificially induced autopolyploid with its diploid progenitor under a variety of conditions. Autopolyploids derived from all of the other species failed completely. Consequently, the results of this experiment can be interpreted as indicating the maximum success that the non-hybrid autopolyploid of a grass species can achieve in a semi-natural habitat in comparison with its diploid progenitor.

The fact should be emphasized that the experiment to be reviewed below was not a single, isolated effort. It was, rather, the most successful of a series of attempts to establish in nature artificially induced tetraploids belonging to several different and diverse genera.

In all, 22 different plantings were made of diploid and autotetraploid *Ehrharta*, some of which consisted of seed sown in plots 5 × 5 m², the diploid plot being sown adjacent to that of the tetraploid, while others were started by planting well-rooted clonal divisions, in which diploids and tetraploids alternated with each other. As shown previously (Stebbins, 1949), distinctive morphological characters enabled me to follow the spread or extinction of diploids and tetraploids, but from time to time these results were checked by actual chromosomal counts. Sixteen of the plots were on the campus of the University of California, Berkeley, and two each in the inner Coast Ranges of Napa County, the campus of

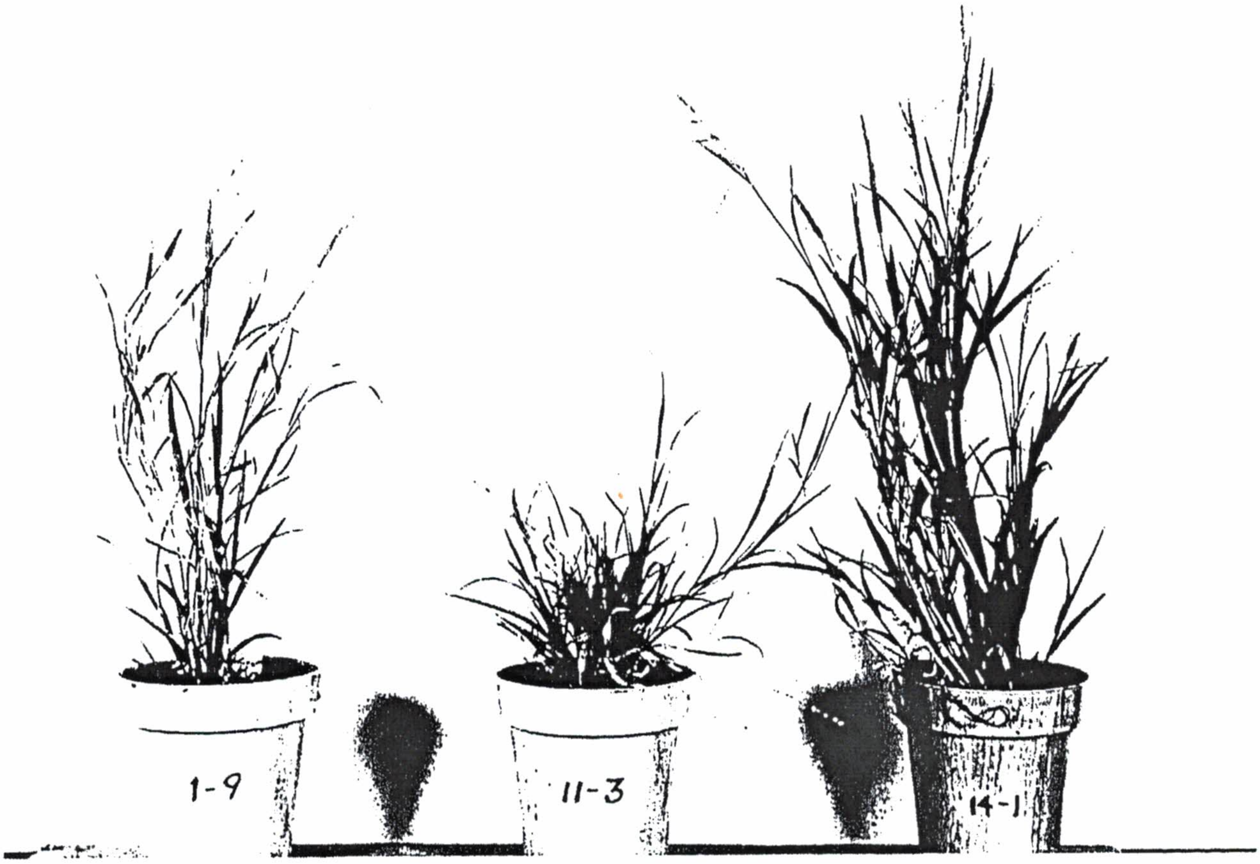

FIGURE 1. Three plants of *Ehrharta erecta,* descendants of the planting made in 1943, dug in 1972 in the neighborhood of Plot 7, Strawberry Canyon, Berkeley and growing under uniform conditions in a greenhouse, 1973. At left a plant from the original diploid planting; center, a plant from about 30 m up the hill, in beaten ground under a picnic table; at right, a plant from about 100 m away, in deep shade of a planted redwood grove. All of these plants are diploid; variation of this kind was not observed among the tetraploids.

the University of California at Santa Cruz, and the town of Carmel, Monterey County.

Although diploid *E. erecta* has survived and is reseeding itself in most of the plots, and from some of them has spread extensively into surrounding areas, the autotetraploid has failed completely except in two of them, both of them in Strawberry Canyon near Berkeley's Botanical Garden. The one described as Plot 7 in the previous account (Stebbins, 1949) has been followed for 39 years. Up until 1948, the tetraploid was more successful there than was the diploid. A few years later a small building was erected just below this plot, and apparently dirt from the excavation that contained seeds of *Ehrharta* was thrown into a grove of oaks where no planting had been made. This condition was first noticed in 1957, and the frequency of diploids and tetraploids was determined in the accidentally seeded lower area in 1965. In the area as a whole, the number of established plants was: diploids 200, tetraploids 230. The distribution patterns of the two cytotypes was highly distinctive: as in the originally seeded upper plot, the tetraploid plants were concentrated in that portion of the area that occupied the steepest, best drained slope, and was most heavily shaded under *Quercus agrifolia.* For several years after these observations were made, little change was noticed, but about 1965 *Ehrharta* spread extensively westward. The plants colonized relatively diverse areas, some of them in hard packed soil and others in well-drained areas under redwoods (*Sequoia sempervirens*). In 1972 these areas were plotted and the most extreme types, including some that resembled the original tetraploids, were taken to the greenhouse for chromosome counting. All of them proved to be diploids. Nevertheless, some of them maintained their characteristic growth habits under uniform conditions, as shown in Figure 1.

The first plot planted in 1943 and the second pair of plots established in 1964 show similar results. In both areas, the diploid has spread ex-

tensively and the autotetraploid, although it still maintains itself, has remained in the type of habitat that exists where it was first established, and has decreased in numbers.

The relative lack of success of tetraploid *E. erecta* during the long period of the principal experiment cannot be ascribed to low seed fertility. Although precise records of seed fertility have not been kept, it has consistently been higher than 80%, and during the first years of the experiment, large numbers of seedlings were found every year near the mother plants.

These experiments should not be interpreted to mean that autopolyploids are always inferior to allopolyploids as colonizers of new habitats. Those that are derived from hybridization between genetically compatible ecotypes of the same species, or between genetically different diploid genotypes that exhibit good combining ability may often be superior to their parents. This conclusion is supported by the experience of agronomists who have attempted to breed new autotetraploids of commercial value. The most extensive efforts in this direction have been made by Müntzing (1954) with cereal rye. He has achieved success only by intercrossing cultivars either at the original diploid level or their induced tetraploids, in order to increase the base of genetic diversity. Dealing chiefly with alfalfa (*Medicago sativa*), Bingham (1980) has emphasized further the importance of hybridization and heterozygosity for the production of successful autopolyploids. How does this relate to the situation in nature?

Polyploidy Among Species That Have Recently Colonized New Areas

Except for intentional attempts at introduction, like that just described for *Ehrharta,* the most direct evidence available that bears on the problem can be obtained by comparing chromosome numbers of the same species or closely related species pairs, some populations of which are in their original native habitat, while others have been introduced in historical times into a new region. Recent spontaneous allopolyploidy is known for two such examples: *Spartina townsendii* (*S. maritima* × *alterniflora*) (Marchant, 1966) and *Tragopogon mirus* plus *T. miscellus* (Ownbey, 1950). These examples show that new allopolyploids can often be highly successful. On the other hand, a large number of diploid species have become adventive and established in large populations as adventives on continents different from their original homes. In many of them, diploid chromosome numbers have been counted both in their original home and on the continent where they are adventive. Fingering through the chromosomal encyclopedia edited by Fedorov (1969), I find 14 such examples in the Gramineae (Poaceae) alone. Admittedly, this evidence is weak. If autopolyploids of adventive species, originating recently, had still a much restricted geographic distribution they could easily be overlooked. Nevertheless, in some genera, such as *Tragopogon,* in which even the diploids have very large achenes, the increase in size that would certainly accompany autopolyploidy would be likely to receive attention. A reasonably safe statement is that in *Tragopogon* species established as adventives in the New World, allopolyploidy has been a more successful evolutionary change than autopolyploidy.

Another kind of indirect evidence is derived from comparing the frequency of polyploidy in neighboring genera of the same family, or in different subgenera of the same genus. If the source of polyploid series is autopolyploidy in which the change in chromosome number is the chief reason for success, no difference would be expected between these closely related groups, particularly if they have similar geographic and ecological distributions. On the other hand, if a major reason for success depends upon generating and maintaining favorable new gene combinations following hybridization between previously separated populations in areas of secondary contact, then the frequency and success of polyploids in a genus or subgenus should be positively correlated with the number of secondary contacts that have been made during its evolutionary history. This number would obviously be greater for groups that, because of their ecological preferences, tend to have a "patchy" distribution than for those that contain species that are distributed chiefly in more continuous habitats such as climax forests and riverine habitats.

Two families that exhibit, in a dramatic fashion, the pattern predicted on the basis of the secondary contact hypothesis are the Salicaceae and Betulaceae. In the Salicaceae, species of *Populus* are mostly confined to the margins of streams and rivers, and so exhibit continuous distribution patterns. All of the established species are diploid, although individual polyploid trees are not uncommon. On the other hand, the species of *Salix* include both riverine species and those

that have patchy distributions in early stages of forest succession or on mountain slopes. Among them are many polyploids, having chromosome numbers as high as $2n = 190$ (Fedorov, 1969). In the Betulaceae, the genera *Carpinus, Corylus,* and *Ostrya* grow in well-developed continuous forests, often on stream margins. All but one are diploid. Species of *Betula* grow in a variety of habitats, but many of them are found principally on mountain slopes and in bogs, and therefore patchy distribution patterns were likely to have been found also in the past. Of the 37 species of *Betula* that have been counted, 19 are polyploid or contain polyploid cytotypes, their polyploidy being well correlated with ecological preferences that would favor patchy distribution patterns.

Another family that provides evidence of this kind is the Liliaceae. Among forest loving genera like *Lilium, Disporum,* and *Trillium,* polyploid series are rare. Related genera, having species adapted to more open, patchy habitats like *Tulipa, Gagea,* and *Lloydia* contain high percentages of polyploid species and cytotypes.

Among the Gramineae, differences of this kind are rare, since nearly all of the larger genera contain high percentages of polyploids. Nevertheless, suggestive patterns exist in the subfamily Bambusoideae, that have been carefully analyzed by Soderstrom and his associates (Soderstrom, 1981; Hunziker et al., 1982). Bamboos are of particular importance in this connection, since they are confined to mesic forests or forest margins, almost entirely in the tropics, and never in climates or situations characterized by extremes of drought or cold. Soderstrom divides the subfamily into two groups: the woody bamboos, containing chiefly the tribe Bambuseae; and the herbaceous bamboos, that resemble typical bamboos in most of their reproductive characteristics but are low growing, herbaceous, and confined to the understory of tropical rain forests. They include several tribes. Assuming that basic gametic numbers are $x = 12$, 11, and 10 (the probable polyploid origin of these numbers is discussed later in this article), the 108 woody species that have been counted include 86 tetraploids and 18 hexaploids making 96% polyploidy, while the 35 herbaceous species include six tetraploids, or 17%. A further point of great importance is that within the woody group the same level of polyploidy exists within entire genera or groups of genera, while two of the herbaceous genera include both diploids and tetraploids.

These differences are best explained by assuming that the polyploidy among the woody group is more ancient than among the herbaceous group, in agreement with conclusions about woody angiosperms in general, as compared to herbaceous groups (Stebbins, 1980; Ehrendorfer, 1980; Raven, 1975). The hypothesis is that arboreal bamboos first became differentiated in forest margins, perhaps in montane regions, where patchy distributions and frequent secondary contact promoted the success of hybrid polyploids. These became the ancestors of modern genera and tribes. More recently, successful species of woody bamboos have become incorporated into forest floras, have reduced tendencies for colonization and secondary contact, and so do not exhibit polyploid series. Herbaceous bamboos, on the other hand, have always been adapted principally to the understory of rain forests, but from time to time have become colonizers in connection with which they have given rise to a few polyploid species within genera that still contain diploids.

The implications of this hypothesis are far-reaching. First, the success of polyploid cytotypes, species, and genera is connected only indirectly to increase in chromosome number per se and is due primarily to favorable gene combinations that they contain. As I have repeatedly emphasized elsewhere (Stebbins, 1950, 1980), polyploidy throughout the continuous spectrum that extends from auto- to allopolyploidy buffers and tends to preserve favorable gene combinations, particularly those in which adaptive fitness depends largely upon heterozygosity and epistatic gene interactions. Buffering is achieved in two different ways: tetrasomic inheritance ratios and preferential pairing of completely homologous chromosomes, i.e., those having identical or very similar nucleotide sequences in their DNA. These mechanisms have been described in numerous publications, including those that have been cited, and need not be repeated here.

The secondary contact hypothesis predicts that isolated polyploid races as well as localized autopolyploid cytotypes should be found in many diploid or homoploid species: this prediction is in accord with presently available data. On the other hand, the difference between failure, localized establishment, and widespread success depends not upon changes in chromosome number but upon acquisition of favorable gene combinations. Although these may sometimes arise by mutation alone, they are much more likely to arise among the diverse segregants that arise after

hybridization between previously isolated and adaptively differentiated populations. These populations may be interfertile races of the same species so that polyploid segregants from their hybrid would be autopolyploids. Other diploid ancestors may belong to distinct species that form sterile hybrids at the diploid level so that polyploid derivatives would incorporate various degrees of allopolyploidy. Again, what counts is the adaptiveness of population environment interactions, not the taxonomic status of parental populations.

CYCLES OF POLYPLOIDY IN THE GRAMINEAE

As stated in the introduction, one reason for unusually high levels of polyploidy in Gramineae is the frequent establishment of polyploid basic numbers after an initial cycle of polyploidy followed by diploidization. This condition is best interpreted by assuming that within the same genus occur successive cycles of polyploidy, between which evolution takes place at homoploid levels. The secondary contact hypothesis would predict that these cycles would coincide with periods when maximal probabilities existed for separation, differentiation and later reunion of populations. Does the evolution of the family as we know it agree with such a prediction?

Unfortunately, the fossil record is too incomplete to provide a definite answer to this question. Nevertheless, shifts in paleoclimates, particularly at the end of the Cretaceous and throughout the Tertiary Period, lend support to this assumption. In agreement with most modern discussions of the phylogeny of the family, I assume that the earliest grasses inhabited margins of tropical forests, then invaded open tropical savannas, entered still later into expanding temperate grasslands during the middle and end of the Tertiary Period, and finally occupied weedy habitats created by human disturbance after the retreat of the Pleistocene glaciers.

The first cycle of polyploidy occurred probably soon after the family originated in the Upper Cretaceous Period. From the widespread initial base numbers of $x = 6$ and 5 arose in different groups the secondary base numbers $x = 12$ and 11. The following facts support retention of the hypothesis that the base numbers $x = 10$, 11, and 12 are not primitive as suggested by Raven (1975), but derived by polyploidy from $x = 5$ and 6. First, they appear in a few distantly related groups that are among the most primitive genera of their tribes, such as *Danthonia* and *Pentaschistis* in the Danthonieae, as well as *Elionurus* (Kammacher et al., 1973) and *Sorghum* in the Andropogoneae. Second, the alternative hypothesis proposed by Raven that $x = 7$, 6, and 5 are derived by aneuploid reduction from $x = 12$ is made improbable by the extreme rarity of $x = 8$ in the family as a whole, and the almost equal rarity of $x = 9$ except in highly specialized members of the Paniceae and Erogrosteae. The early cycles of polyploidy may well have been associated with mountain building "revolutions" that took place at the end of the Cretaceous Period and brought about many shifts in the location of forests and forest margins. The second cycle may have coincided with the opening up of warm savanna habitats during the Eocene epoch, particularly in South America, where the first grazing mammals evolved (Andreis, 1972; Patterson & Pascual, 1968). Fragments of siliceous bodies found in Eocene loess deposits of South America are most probably remnants of Eocene grasses (Frenguelli, 1930). Entrance into north temperate habitats is documented partly by the numerous fossil grass seeds that have been found on the plains of North America (Stebbins, 1950; Thomasson, 1978) and may well have coincided with shifts in position, expansion, and contraction of temperate grasslands. These events were followed by extensive mountain building throughout the world during the Pliocene epoch creating, in the Northern Hemisphere, the continental type of climate characterized by great seasonal differences in temperature to which the majority of genera belonging to the tribe Festuceae are adapted. New polyploids probably arose more or less continuously during the Pliocene and Pleistocene epochs, their evolution being stimulated by the advances and retreats of the Pleistocene glaciers and the shifts in vegetation that accompanied them. A final cycle of polyploidy, affecting chiefly weedy genera like *Bromus, Triticum* (*Aegilops*), *Hordeum, Eragrostis, Chloris,* and *Digitaria,* took place in association with human disturbance and cultivation since the retreat of the glaciers and the onset of warmer climates through much of the world. In my opinion, Gramineae contain higher percentages of polyploids, both primary and secondary, than do other families of angiosperms because their favored habitats and methods of reproduction preadapted them particularly well for taking advantage of the climatic cycles just outlined.

SUMMARY AND CONCLUSIONS

The percentage of species having had polyploid events during their evolutionary history is in the Gramineae between 80 and 90%, the highest of any large angiosperm family. This includes both polyploid series within genera and ancient polyploidy that gave rise to high basic diploidized numbers for many genera. The evidence presented indicates that this high percentage exists not because the grass genome is more prone than others to the occurrence of polyploid individuals within populations or that raw autopolyploids are in any way superior to their diploid progenitors, but because frequent opportunities for secondary contact and hybridization between differentiated diploid populations have generated highly adapted, aggressive gene combinations that have been buffered and maintained largely by the effects of polyploidy in favoring tetrasomic inheritance and preferential pairing of homologous, as compared to partly homologous (homeologous), chromosomes.

1. Comparison between artificially produced autopolyploids and their diploid ancestors, particularly an experiment of 39 years' duration with *Ehrharta erecta,* has shown that without hybridization, autopolyploids, even when highly fertile, are greatly inferior to their diploid progenitors under field conditions or at best can maintain themselves but lack aggressiveness and the ability to invade new habitats.

2. The hypotheses advanced by early workers that polyploids owe their success to their greater ability to withstand severe ecological conditions, such as cold and drought, have been refuted by recent data showing that polyploids are nearly or quite as successful under favorable mesic tropical conditions as in arid and cold regions.

3. Comparing genera in various families, some having high and others low frequencies of polyploidy, a correlation is found between high frequencies of polyploidy and patchy geographical or ecological distributions, which have permitted many secondary contacts between differentiated populations.

The secondary contact hypothesis just proposed is supported also by the fact that throughout the geological periods during which the family Gramineae has evolved, habitats favored by grasses such as forest margins, savannas, temperate grasslands, and arctic-alpine tundra have become alternately extended and localized and have changed their geographic positions. These successive habitat changes have promoted the successive cycles of polyploidy that are needed to explain both the high frequency and the high levels of polyploidy found in the family.

LITERATURE CITED

ANDREIS, R. R. 1972. Paleosuelos de la formacion Musters (Eocene medio), Laguna del Mate, Prov. de Chubut., Rep. Argentina. Rev. Asoc. Arg. Mineral. Petrol. Sedimentol. 3: 91–97.

BINGHAM, E. T. 1980. Maximizing heterozygosity in autopolyploids. Pp. 471–490 *in* W. H. Lewis (editor), Polyploidy, Biological Relevance. Plenum Press, New York and London.

BROCK, R. D. & J. A. M. BROWN. 1961. Cytotaxonomy of Australian *Danthonia.* Austral. J. Bot. 9: 62–92.

DARLINGTON, C. D. 1973. Chromosome Botany and the Origins of Cultivated Plants, 3rd edition. Allen and Unwin, London.

DEWEY, D. R. 1970. Genome relationships among diploid *Elymus junceus* and certain tetraploid and octoploid *Elymus* species. Amer. J. Bot. 57: 633–639.

EHRENDORFER, F. 1980. Polyploidy and distribution. Pp. 45–60 *in* W. H. Lewis (editor), Polyploidy, Biological Relevance. Plenum Press, New York and London.

FAVARGER, C. 1957. Sur le pourcentage des polyploides dans la flore de l'étage nival des Alpes Suisses. Compt. Rend. 8th Congr. Int. Bot. (Paris) 9–10: 51–58.

FEDOROV, A. A. (editor). 1969. Chromosome Numbers of Flowering Plants. Izdatelstvo "Nauk," Leningrad.

FRENGUELLI, J. 1930. Particulas de silice organizada en el loess y en los limos pampeanos. Selulas siliceas de Gramineas. Anales Soc. Ci. Santa Fé 2: 1–47.

GOULD, F. W. 1966. Chromosome numbers of some Mexican grasses. Canad. J. Bot. 44: 1683–1696.

GUSTAFSSON, A. 1948. Polyploidy, life form and vegetative reproduction. Hereditas 34: 1–22.

HARTUNG, M. F. 1946. Chromosome numbers in *Poa, Agropyron* and *Elymus.* Amer. J. Bot. 33: 516–532.

HUNZIKER, J., T. SODERSTROM & A. F. WULFF. 1982. Chromosome numbers in the Bambusoideae (Gramineae). Brittonia 34: 30–35.

KAMMACHER, P., G. ANOMA, E. ADJANOHOUN & L. AXE-ASSIL. 1973. Nombres chromosomiques de Gramines de Cote-d'Ivoire. Candollea 28: 191–217.

LÖVE, A. & D. LÖVE. 1949. The geobotanical significance of polyploidy. I. Polyploidy and latitude. Portugaliae Acta Biol., Sér. A, Special Vol. R. B. Goldschmidt: 273–352.

MARCHANT, C. 1966. The cytology of *Spartina* and the origin of *S. Townsendii.* Pp. 71–72 *in* C. D. Darlington & W. L. Lewis (editors), Chromosomes Today. Volume 1. Oliver and Boyd, Edinburgh and London.

MÜNTZING, A. 1954. An analysis of hybrid vigour in tetraploid rye. Hereditas 40: 265–277.

Ownbey, M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon*. Amer. J. Bot. 37: 487–499.

Patterson, B. & R. Pascual. 1968. The fossil mammal fauna of South America. Quart. Rev. Biol. 43: 409–451.

Raven, P. H. 1975 [1976]. The bases of angiosperm phylogeny: cytology. Ann. Missouri Bot. Gard. 62: 724–764.

Reese, G. 1958. Polyploidie und Verbreitung. Z. Bot. 46: 339–354.

Soderstrom, T. R. 1981. Some evolutionary trends in the Bambusoideae (Poaceae). Ann. Missouri Bot. Gard. 68: 15–47.

Stebbins, G. L. 1949. The evolutionary significance of natural and artificial polyploids in the family Gramineae. Proc. 8th Int. Congr. Genetics (Hereditas, Suppl. Vol.), pp. 461–485.

———. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

———. 1972. The evolution of the grass family. Pp. 1–17 *in* V. B. Younger & C. B. McKell (editors), The Biology and Utilization of Grasses. Academic Press Inc., New York and London.

———. 1975. The role of polyploid complexes in the evolution of North American grasslands. Taxon 24: 91–106.

———. 1980. Polyploidy in plants: unsolved problems and prospects. Pp. 495–520 *in* W. H. Lewis (editor), Polyploidy, Biological Relevance. Plenum Press, New York and London.

Thomasson, J. R. 1978. Epidermal patterns of the lemma in some fossil and living grasses and their phylogenetic significance. Science 199: 975–977.

Tischler, G. 1935. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erlautert an den Arten Schleswig-Holstein, mit Ausblicken auf andere Florengebiete. Bot. Jahrb. Syst. 67: 1–36.