

by the writer furnished abundant material. All specimens cited are in the Bishop Museum. The accompanying drawing was made from fresh material by Florence Mekeel.

This new species is named in warm tribute to Professor Merritt Lyndon Fernald, my principal teacher of botany. His devotion to science, tireless research, originality, arduous but joyous field exploration, broad scholarship, and vivid inspiring teaching are known to all systematic botanists. At least one other Hawaiian plant already bears his name, for J. F. Rock described a handsome shrub in the Lobeliaceae as *Cyanea Fernaldii*, in Mem. Bishop Mus. vii (2): 235-237, Pl. 128, 1919.

EXPLANATION OF PLATE

PLATE 3. *PLEOMELE FERNALDII* St. John, habit and flowers from type, Mahana, Lanai, *St. John & Cowan* 22,666. Fig. a, habit $\times \frac{1}{4}$; Fig. b, flower, $\times 1$; Fig. c, flower, $\times 1$; Figs. d, e, berry, $\times 1$, from Kamoku, Lanai, *St. John & Cowan* 22,602; Figs. f, g, seeds of same, $\times 1$.

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THE ORIGIN OF THE COMPLEX OF *BROMUS* *CARINATUS* AND ITS PHYTOGEOGRAPHIC IMPLICATIONS

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Both cytogenetic experiments in the laboratory and studies of wild species in nature have now established firmly the fact that in the higher plants sterile hybrids between distantly related species have very frequently been converted into fertile, constant, self-reproducing species by the process of doubling the chromosome number, or polyploidy. These hybrid polyploids, or allopolyploids, are often more vigorous than either of their parental species, and may therefore acquire geographical distributions which range far beyond those of their parents. They may exist as species for geologic ages, and in fact outlast their parental species. Furthermore, allopolyploids often tend to occupy areas which are newly opened to colonization by plants, and to leave their parental species in possession of the geologically older, relict areas. One effect, therefore, of changes in the earth's surface on its flora will be to eliminate the diploid species from many regions, and to leave only the more vigorous, better adapted allopolyploid species derived from them. The data on which

these postulates are based are reviewed elsewhere by the writer (Stebbins 1940, 1942, 1947a).

As pointed out by the writer in a previous publication (Stebbins 1942), this ability of allopolyploids to spread beyond and to outlast their diploid ancestors provides botanists with a new and valuable tool for studying the past history and migrations of floras. By a combination of insight and deduction, careful systematic study, and cytogenetic experimentation, we can often identify the diploid ancestors of an allopolyploid species, or at least their nearest living diploid relatives or descendants. If diploids and allopolyploid derivatives still occur together in the same region, we can assume that the latter arose under conditions essentially the same as those now prevailing. But if the present distribution of the allopolyploid proves to be different from that of its diploid relatives, and particularly if the representatives of the two original parents of an allopolyploid now occur in regions remote from each other, then we must assume that at the time when the allopolyploid arose, the distribution of these ancestral types was different from what it is at present. And by viewing the present distributions of the species concerned in the light of past events of geological history and of the distribution of fossil floras, we can often make good inferences as to the time and place of origin of the allopolyploid, and therefore of the past distribution of its parental types. The studies of Anderson (1936) on the origin of *Iris versicolor*, of Camp (1944) on that of *Oxycoccus quadripetalus*, and of Johnson (1945) on the origin of *Oryzopsis asperifolia* and *O. racemosa* are all examples of the successful use of this tool. (Stebbins 1947b).

A group of grasses particularly well suited to this type of analysis is the section *Ceratochloa* of the genus *Bromus*. Previous studies (Stebbins and Tobgy 1944) have shown that the species of this section can with one exception be divided into two series on the basis of their chromosome complements, which run parallel with certain morphological characteristics and with geographic distribution. With the exception of *B. arizonicus* (Shear) Stebbins, which has 84 chromosomes (Stebbins, Tobgy, and Harlan 1944), all of the forms native to North America which the writers had counted were octoploids with 56 chromosomes and were of allopolyploid origin. Those known from South America, on the other hand, were uniformly hexaploid, with 42 chromosomes, and although also allopolyploid, were assumed to be more ancient.

Chromosome behavior in hybrids between North American forms and those native to South America had uniformly 21 pairs of chromosomes, and 7 univalents, the latter being of larger size than the former. The chromosome formula of the South American *B. catharticus* Vahl and its relatives was given as AABBC and that of *B. carinatus* H. & A., *B. marginatus* Nees, and their North American relatives as AABBCCL. The set designated as L consists of seven relatively large chromosomes, corresponding in number, size, and morphology to those found in various species of the section *Eromopsis*, such as *B. laevipes* Shear, *B. vulgaris* Shear, and some forms referred to *B. ciliatus* L. Furthermore, in the diagnostic characteristics of the spikelets, particularly the lemmas and caryopses, *B. carinatus* and its relatives are intermediate between the South American *Ceratochloas* and the diploid species of the section *Bromopsis*. The hypothesis was therefore advanced by the writer (Stebbins and Tobgy 1944) that the octoploid North American *Ceratochloas* arose as allopolyploids from hybrids between ancestral species similar to *B. catharticus* and diploid *Bromopsis* species related to *B. laevipes*, *B. vulgaris*, and *B. ciliatus*.

HYBRIDS BETWEEN SPECIES OF SECTIONS CERATOCHLOA AND BROMOPSIS

The direct testing of this hypothesis by crossing *B. catharticus* with species of the section *Bromopsis* has proved technically difficult for several reasons. In the first place, *B. catharticus*, at least under the conditions prevailing in Berkeley, shows an even stronger tendency than *B. carinatus* to produce the type of cleistogamous flowers described by Harlan (1945), and these are useless for emasculation and cross pollination. Chasmogamous flowers with large anthers are usually produced only relatively early in the season, before the beginning of the normal period of flowering of the species of *Bromopsis* available to us. Furthermore, all of the *Bromopsis* species available can be crossed with *B. catharticus* and its relatives only with the greatest difficulty. One hybrid between *B. catharticus* and *B. laevipes*, produced in 1944, proved to be a very weak plant. In spikelet characteristics it matched fairly well some forms of *B. marginatus*. It was completely sterile. Since all of the florets produced were of the cleistogamous type with small anthers, meiosis could not be studied in it. An attempt to double its chromosome number with the aid of colchicine resulted in the death of the plant. No similar hybrids have since been produced.

Another type of hybrid which could provide indirect but nevertheless strong evidence on the origin of *B. carinatus* and its relatives consists of those between these octoploids and diploid species of the section *Bromopsis*. Because of the great difference in chromosome number, success was not at first expected from such crosses. But in 1945 a single pollination of 60 florets of a strain of *B. marginatus* from Meadow View Ranger Station,



Figure 1. Typical first metaphase plate in *Bromus marginatus* x *laevipes*, no. 603-1, showing 7 large bivalents, one loosely associated medium-sized bivalent, and 19 medium-sized univalents.

Plumas County, California, with a strain of *B. laevipes* from north of Castaic, Los Angeles County, yielded two hybrid plants. Their initial growth was slow, but they bloomed freely in 1946, and in 1947 were exceptionally vigorous. They are completely sterile as to both pollen and seed. Morphologically, they resemble more nearly *B. marginatus*, but the panicle is more ample, with very numerous spikelets, and the lemmas are less carinate, and somewhat more hirsute.

These hybrids have the expected chromosome number, 35, in their somatic cells. At meiosis, the seven large chromosomes

derived from *B. laevipes* are usually paired with the L set from *B. marginatus*, and the 21 medium-sized ones are unpaired except for one to four loosely associated rod-shaped bivalents, and rarely a single bivalent with a chiasma in both arms of the chromosomes. Analysis of 50 sporocytes at first metaphase is given in table I, and a typical configuration is shown in figure 1.

Table I. Frequency distribution of sporocytes with different numbers of large and medium-sized bivalents in 50 sporocytes of *Bromus marginatus* $\times$ *laevipes*, no. 603-1.

									Total
Number of bivalents.	0	1	2	3	4	5	6	7	Bivalents
Frequency, L bivalents.	0	0	0	0	1	10	14	25	313
Frequency, M bivalents.	4	13	20	9	3	0	1		98

These results show that there is a strong homology between the chromosomes of *B. laevipes* and the L set of *B. marginatus*, and therefore support the hypothesis presented above as to the origin of the latter. The small amount of pairing between chromosomes of the medium-sized type is similar to that found in haploid plants of wheat (*Triticum aestivum*) and many other plants, and is probably due to the presence of duplications of segments, rather than to homology of whole chromosomes.

Nevertheless, the pairing of the L chromosomes of this hybrid is much less regular than is that of the M type in hybrids between *B. catharticus* and *B. carinatus* or *B. marginatus* (Stebbins and Tobgy 1944). The percentage of potential bivalents that are unpaired is 10.6%, or 100 times as great as in *B. catharticus* $\times$ *B. marginatus* or *B. carinatus*, and also much greater than in hybrids between *B. carinatus* and *B. marginatus*. Furthermore, the bivalents themselves are much more loosely paired than in any of the previous hybrids. Of the 313 bivalents observed, 158, or 50 per cent, are of the rod type with a single chiasma. In the hybrids between *B. catharticus* and *B. carinatus* or *B. marginatus*, only 1 to 3 per cent of the bivalents were of this type, a proportion similar to that found in *B. catharticus* itself.

These results indicate that *B. marginatus* and its relatives are allopolyploids derived from hybridization between hexaploid species of the section *Ceratochloa* related to *B. catharticus* and diploid species of the section *Bromopsis*, but these diploids were not very closely related to the modern *B. laevipes*. This explanation is also supported by the difficulty of hybridization between *B. laevipes* and *B. catharticus*. Whether other modern diploid species of *Bromopsis* are more nearly related to the ancestor of

B. marginatus than *B. laevipes* cannot be decided at present. Dr. D. D. Miller (unpubl.) found 4 to 7 per cent of the potential bivalents unpaired in hybrids involving *B. laevipes*, *B. Orcuttianus*, and *B. grandis*, while the writer (unpubl.) found complete pairing in all of 30 sporocytes of *B. Porteri* $\times$ *vulgaris*. Present evidence, therefore, indicates that the chromosomes of the modern western American species of the section *Bromopsis* may all be more similar to each other than any of them are to the *Bromopsis* genome found in *B. marginatus*.

THE RELATIONSHIPS AND DISTRIBUTION OF THE NEW WORLD SPECIES OF SECTIONS *CERATOCHLOA* AND *BROMOPSIS*.

The present distribution and relationships of the *B. carinatus* complex and its ancestors can be described as follows. The hexaploids of the section *Ceratochloa*, which contain the A, B, and C genomes, are now widespread in and endemic to the temperate parts of South America, including the entire cordillera of the Andes from Venezuela to Tierra del Fuego. Although they have been referred by some systematists to a single species, *B. catharticus* or *B. unioides*, unpublished genetic evidence of the writer indicates that at least three or four distinct species are present. These form F_1 hybrids which are vigorous and have good pairing of the chromosomes at meiosis, but which are highly sterile. At present, there is no certainty as to which of these species is the most nearly related to the ancestor of the *B. carinatus* complex, but some evidence suggests that the species with relatively long awns, found in central Chile and the southern Andes, namely *B. stamineus* Desv. and *B. coloratus* Steud., are the most likely. These resemble *B. carinatus* much more nearly than do the short-awned types like typical *B. catharticus*; and a hybrid between *B. stamineus* and *B. marginatus* has yielded a relatively fertile allopolyploid, while the polyploids derived from hybrids between *B. catharticus* and either *B. marginatus* or *B. carinatus* are highly sterile.

The other set of ancestors of the *B. carinatus* complex, the diploid species of the section *Bromopsis*, are concentrated in western North America. As far as is known, their chromosomes are so similar that a high degree of pairing occurs in their F_1 hybrids. There are also several species of the section *Bromopsis* in South America, occurring together with the hexaploid species of section *Ceratochloa*, but those which have been investigated, and they include all of the widespread and common South American species of this section, are themselves polyploid. The number

$2n = 42$ was counted in cultures of *B. auleticus* Trin. and *B. uruguayensis* Arech., grown from seed sent by Sr. Bernardo Rosengurtt from Uruguay, while *B. macranthus* Desv., sent by Sr. Edmundo Pisano (no. 2014) from the Andes of Central Chile, had $2n = 28$.

Measurements of the size of stomata and pollen have been made on several herbarium specimens of these and other South American species of this section, and they indicate the presence of polyploid numbers in all but two specimens. These putative diploids are *Hitchcock 22530*, from above Ollantaytambo, Dept. Cuzco, Peru, and one culm of *Hitchcock 22776*, from Pongo, Nor-Yungas, Bolivia: The specific identity of both of these specimens is uncertain.

As mentioned above, the complex of octoploids consisting of *B. carinatus*, *B. marginatus*, and their relatives are the most widespread and common native species of *Bromus* throughout western North America, from Alaska to Guatemala. The number of species present in this group has been subject to widely different interpretations by the different systematists who have treated it, and genetic evidence obtained by the writer is not helping to solve this problem. The evidence produced by Stebbins and Tobgy (1944) suggested that at least the *B. carinatus* strains of coastal California and the *B. marginatus* of Arizona are separated by barriers of almost complete hybrid sterility and should be placed in separate species. But more recently hybrids between either of these extremes and types from intermediate localities have proved to be partially fertile, and to yield offspring in the F_2 generation which are highly so. More complete data, therefore, may demonstrate that most of the strains of this octoploid complex are interconnected by forms with which they can form at least partly fertile hybrids. This situation is an anomalous one, which, so far as the writer is aware, has not been described for any other wild species. It is somewhat similar to that described by Terao and Midusima (1939), cf. Stebbins (1942b) in cultivated rice.

Several new chromosome counts have been made in this group, all of them $2n = 56$. No material has yet been obtained from Alaska, but one collection made by Dr. J. Harlan near Mexico City, and another from Quetzaltenango, Guatemala, both of which are referable to *B. laciniatus* Beal, have 56 chromosomes, and the A, B, C, and L sets can be recognized in them. Every possible effort has been made to secure material of the strains of this group on which the reports in the literature of numbers lower

than 56 have been based (cf. Stebbins and Tobgy 1944), but these have been unsuccessful. In the writer's opinion, no such strains exist as native plants in North America. The number $2n = 70$, reported by Nielsen (1939) for *B. marginatus* from Wyoming, has not been found either; apparently strains with this number are rather restricted in distribution.

The occurrence in South America of species of *Bromus* having 56 chromosomes and the constitution AABBCCLL was discovered in a seed sample received as *B. coloratus* Steud., from Sr. Bernardo Rosengurtt of Juan Jackson, Uruguay, and originally collected in the Nahuel Huapi National Park, in the Andes of southern Argentina. Comparison of plants grown from these seeds with a large series of specimens borrowed from the U. S. National Herbarium through the kindness of its curator, and with the helpful assistance of Mrs. Agnes Chase, showed that they differ in several respects from typical *B. coloratus*. Characteristic plants of the latter species were grown from another seed sample sent by Sr. Rosengurtt, and were found to have 42 chromosomes and the AABBCCLL constitution typical of South American representatives of the section *Ceratochloa*. The octoploid from Nahuel Huapi, on the other hand, resembles in its habit, inflorescence, and lemmas specimens from Bolivia (Sorata, 4000 m., Lacatia, *Günther* 85; Sorata, *Holway* 552) which were identified by Dr. A. S. Hitchcock as *B. pitensis* H. B. K. Both these Bolivian specimens and several of typical *B. pitensis* from Ecuador agree with the octoploid from Nahuel Huapi as well as *B. carinatus* and other North American octoploids in the size of their pollen grains and stomata, which are larger than those of the South American hexaploids. It is likely, therefore, that a complex of octoploids with the constitution AABBCCLL exists in the Andes from Ecuador to southern Argentina, which may for the present be placed under the oldest name applied to them, *B. pitensis*. Judging from specimens, however, they are uncommon and very locally distributed except in Ecuador and northern Peru, where typical *B. pitensis* appears to be abundant. In Colombia they are replaced by forms which are apparently indistinguishable from the Mexican and Central American *B. laciniatus*.

An indication of the relationship of these South American octoploids with the North American ones is provided by a hybrid obtained between the *B. pitensis* from Nahuel Huapi and a strain of *B. marginatus* obtained from the nursery of the U. S. Soil Conservation Service at Ames, Iowa, no. M2-9435-42,



which came originally from Colorado. This hybrid was highly sterile and showed much more chromosomal irregularity at meiosis than did any of the hybrids between different North American octoploid types. Among 42 sporocytes analyzed at first metaphase, only 10 had the expected 28 bivalents. Of the remainder, 27 had from 2 to 6 unpaired univalent chromosomes, and 5 had 26 pairs plus a ring or chain of 4. Lagging chromosomes were found in 41 out of 60 sporocytes at first anaphase, and a comparable proportion of tetrads contained extra nuclei or extruded chromatin. Bridge-fragment configurations, resulting from heterozygosity for inversions, were found in 15 sporocytes, or 25 per cent.

A more significant fact is that these irregularities were about ten times as frequent among the large as among the medium-sized chromosomes. Table 2 shows this difference.

Table 2. Relative frequency of meiotic abnormalities in large and medium-sized chromosomes in *Bromus pitensis* $\times$ *marginatus*.

	Large Chromosomes	Medium Chromosomes
Number potential bivalents unpaired	35	10
Per cent potential bivalents unpaired	11.9	1.1
Number bivalents with one chiasma	70	20
Per cent bivalents with one chiasma	23.8	2.3
Per cent bivalents with bridge-fragment configurations	3.6	0.24
Per cent chromosomes lagging at I anaphase	13.1	1.5

Such differences are strong evidence against the hypothesis that *B. marginatus* and *B. pitensis* had a common origin and have diverged relatively recently. Both are allopolyploids derived from hybrids between diploid species of section *Bromopsis* and hexaploids of section *Ceratochloa*, but the *Ceratochloa* parents of these two allopolyploids must have been relatively closely related to each other, and the *Bromopsis* parents much more distantly so. That even the A, B, and C sets of *B. pitensis* are not the same as those of *B. marginatus* is evident from the presence of some irregularities of pairing among the chromosomes of this type, and in particular of the occasional ring or chain of 4 chromosomes, indicating heterozygosity for a translocation involving A, B, or C type chromosomes.

PROBABLE PLACE AND TIME OF ORIGIN OF THE NORTH AMERICAN OCTOPOLOIDS AND ITS IMPLICATIONS

The data presented above make highly probable the assumption that in both North and South America hexaploid species of the section *Ceratochloa*, with the constitution AABBCC, have some time in the past independently hybridized with diploid species of the section *Bromopsis* to produce octoploids similar to *B. carinatus*, *B. marginatus*, and *B. pitensis*. The origin of the South American types cannot be discussed until more is known about them. That of the North American ones is complicated by the fact that only their *Bromopsis* parents occur at present within their range of distribution. *B. catharticus* is found as a recently introduced weed in some parts of this range, but *B. carinatus* and *B. marginatus* were known and recognized before this introduction occurred. The wide distribution of the North American octoploids, and the varied habitats in which they occur indicate that they have been here a long time.

We are forced to conclude, therefore, that some time in the past there existed in western North America as native plants hexaploid species of the section *Ceratochloa* closely related to *B. catharticus*, *B. stamineus*, and *B. coloratus*. The time when this might have occurred is suggested by the studies of Elias (1942) on the fossil grass fruits of the tribe *Stipeae* found by him on the Great Plains. Among such fruits of mid-Pliocene age is a species of the genus *Nassella*, which is now confined to the South American Andes. In addition, the writer has shown elsewhere (Stebbins 1947b) that the bulk of the fruits collected by Elias in deposits of mid-Pliocene age and referred by him to the fossil genera *Stipidium* and *Berriochloa* resemble closely modern species of the genus *Piptochaetium*, subg. *Podopogon*, nearly all of which are now confined to the pampas of eastern South America (Parodi 1944). Seeds of *Bromus*, since they lack the indurated lemma possessed by the *Stipeae*, could not easily become preserved as fossils. But the demonstration that the majority of the known fossil species of grasses of the Pliocene epoch in western North America have their closest living relatives in South America suggests that the same situation was very likely true in *Bromus*, and that at this time hexaploid species of the section *Ceratochloa* occurred here and hybridized with diploid species of section *Bromopsis* to produce the octoploids of the *B. carinatus* complex.

The two problems which remain to be considered are first, the origin and distribution of the hexaploid *Ceratochloas*, and second

the reasons for their extinction in North America. Cytological evidence from several sources indicates that these hexaploids are themselves allopolyploids, derived from hybridization involving three different original diploid species. None of these diploids has yet been found, and examination of stomatal size in a large series of specimens of sect. *Ceratochloa* from South America borrowed from the U. S. National Herbarium failed to reveal any with the small stomata which one would expect in such diploids. These diploid ancestors, therefore, may well be extinct. The evidence from hybrids between different North American octoploids (Stebbins and Tobgy 1944) suggests that the latter arose independently from related but not identical parents, and therefore that more than one ancestral hexaploid may have existed in North America during the Tertiary period. We cannot conclude, therefore, that the present center of distribution of these hexaploids in South America is necessarily the original one, from which they migrated to North America. The only assumption which can be safely made on the basis of the data now available is that during the Pliocene epoch the hexaploid species of *Bromus*, section *Ceratochloa* had either a continuous distribution from temperate western North America to temperate South America, or more probably a bipolar distribution in the temperate zones of the two continents. This latter pattern of distribution is well known in many modern groups of plants, and has been carefully discussed by Johnston (1940) and DuRietz (1940). Its explanation is not yet certain. Both the ancestry and place of origin of the hexaploids, therefore, are at present uncertain.

Two reasons can be suggested for the extinction of the hexaploids in North America during the Pleistocene epoch. In the first place, the climate of temperate North America, because of the greater land mass present, has a much more continental character than that of corresponding latitudes in South America, with lower minimum temperatures in winter, and higher ones in summer. Most of the hexaploid types now existing are adapted to relatively mild winters, and have flourished best as introduced plants chiefly along the Gulf Coast of the southeast, and the coast of California. The climate of western North America during parts of the Pleistocene epoch was more continental than at present, but it may very well have been milder during the Tertiary period, due to the lower elevation of the western Cordillera, and the more extensive ameliorating influence of the Pacific Ocean. The severity of the climate brought on by the Pleistocene

glaciation, therefore, was probably one cause for the extinction of hexaploid species of the section *Ceratochloa* in North America. A second cause may very well have been competition with the vigorous octoploid types which had been newly evolved. These now have "weedy" tendencies, and even in the forested areas spread along roadsides and other areas of disturbed ground. Huskins (1931) has noted the tendency of the newly evolved allopolyploid species *Spartina Townsendii* to drive out its progenitor, *S. maritima*, wherever these two species come into contact with each other. Both of these causes probably contributed to the extinction of the hexaploids, and no decision can be made as to which was the more important.

There is little doubt that other allopolyploids now dominant in North America will be found to be derived from ancestors at present endemic to South America. Their discovery will be a valuable tool for determining the present and past relationships between the floras of the two continents.

SUMMARY

The nature of chromosome pairing in hybrids between *Bromus carinatus* H. & A. or *B. marginatus* Nees and *B. catharticus* Vahl as well as between *B. marginatus* and *B. laevipes* Shear provides strong evidence that the octoploid North American species of *Bromus*, section *Ceratochloa* of which *B. carinatus* and *B. marginatus* are the best known, originated through allopolyploidy involving hexaploid species of section *Ceratochloa*, for which the genome formula AABBCC is used, and diploid species of section *Bromopsis*, having the formula LL. The octoploid South American forms of section *Ceratochloa*, which are tentatively grouped in the species *Bromus pitensis* H. B. K., arose in a similar manner, but independently. Chromosome pairing in *B. pitensis* $\times$ *marginatus* indicates that the A, B, and C genomes of these two species are relatively similar, and therefore that their ancestors in section *Ceratochloa* were closely related, but their L genomes are much more dissimilar, so that their *Bromopsis* ancestors were rather distantly related to each other. Since at present no hexaploid species of the section *Ceratochloa* is native to North America, the distribution of these hexaploids must have been more widespread at the time when *B. carinatus* and *B. marginatus* originated by hybridization and allopolyploidy than it is at present. Evidence from the distribution of fossil *Stipeae* and from the probable nature of the climate in the middle and later part of the Tertiary period suggests that at some time during

this period the hexaploid *Ceratochloa* species and the diploid species of section *Bromopsis* occurred together in western North America. There they hybridized, and their sterile hybrids gave rise by doubling their chromosome numbers to the ancestors of *B. carinatus*, *B. marginatus*, and their relatives. With the onset of the Pleistocene ice age, and because of competition with the more aggressive, newly formed octoploids, the hexaploids became extinct in North America, persisting only in temperate South America, where climatic conditions changed less.

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ENDEMISM IN THE FLORA OF CALIFORNIA

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The most conspicuous feature of the flora of California is the endemism that marks it as distinct from that of most parts of the world. Because of the close inter-relationship among many genera and species, it is puzzling and interesting. Evolution still seems to be progressing since distinctive limits are often so uncertain.

As it would be impossible and impractical to name or even enumerate the endemic species in many genera, because of the diversity of opinion as to criteria for specific limits, the genera only will be considered.

The plan is to take these genera in the order in which the families of plants native in California are generally arranged. Of course, state boundaries mean nothing to plants and it is to be expected that genera distinctly Californian will have species crossing the border. The northern part of Lower California is similar to and really ecologically a part of San Diego County. A similar situation occurs in the adjacent counties of Del Norte, the most northern in California along the coast, and Curry and Josephine counties in southern Oregon. Desert plants cross over into Arizona and Nevada. Nevada also has some of the California species on the east side of the Sierra Nevada boundary.

Among the ferns and fern allies no endemic genera occur. In the Gymnosperms, *Sequoia* Endl. is the only one, with two species growing in limited areas in California, the coast species, *S. sempervirens* (Lamb.) Endl. extending into southern Oregon, adjacent to Del Norte County. This genus was represented in preglacial times by many species in the Northern Hemisphere where their fossil representatives have been unearthed. With the Sequoias are also *Torreya* Arn., *Lithocarpus* Sarg. and *Umbellularia* Nees. The two former have widely separated species



Stebbins, G Ledyard. 1947. "The origin of the complex of *Bromus carinatus* and its phytogeographic implications." *Contributions from the Gray Herbarium of Harvard University* (165), 42–55. <https://doi.org/10.5962/p.336338>.

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