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Polyploidy and the distribution of the arctic-alpine flora: new evidence and a new approach

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Abstract

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The old hypothesis, that polyploids are at a higher frequency in high latitudes because of their greater resistance to the harsh arctic climate is refuted by additional data, comparing frequencies along the Pacific Coast of North America. There, the highest frequency of polyploids is at 52–54° north latitude, while at 63–71° (northern Alaska) the frequency is no higher than in central Europe. There is, however a general correlation between percentages of polyploidy and degree of glaciation during the Pleistocene epoch. Frequencies are also higher at the same latitude in insular regions than on continents, particularly eastern North America. A review of distribution of diploids vs. polyploids within eight genera (*Calamagrostis*, *Campanula*, *Chamaenerion*, *Geum*, *Puccinellia*, *Pulsatilla*, *Salix*, *Saxifraga*) reveals the presence of some diploid species at or near the northern distributional limits of all of them.

Introduction

It gives me great pleasure to dedicate this paper, on his 70th birthday, to my old friend and companion, Claude Favarger, who has made substantial contributions to its topic.

Soon after the concept of polyploidy developed, it was used to explain patterns of plant distribution. The best known early efforts were those of Tischler, who postulated that polyploidy is instrumental in adapting plants to life under the harsh conditions of arctic and alpine regions. His approach to the problem was statistical. He showed that in western Europe, the proportion of polyploid to diploid species increases with latitude. His method was criticized chiefly for two reasons. First, the counts available to him were principally from plants grown in botanical gardens, since at that time very few investigations had been made using fixations from material collected in nature by the investigator. As examples appeared in increasing numbers of species that include cytotypes having different levels of ploidy, the validity of this criticism became increasingly evident. Second, the frequency of polyploidy was found to be correlated with growth habit (Stebbins 1938), and in particular herbaceous perennials, the kind of growth habit that is found in an increasingly high proportion of species as one goes

northward, include relatively high proportions of polyploid species or cytotypes. This introduced a disturbing factor that weakened considerably Tischler's interpretations. Finally Favarger (1957) compared the frequency of polyploidy in the flora of the high alps above the altitude of perpetual snow with that found in the flora of the surrounding lowlands, and found no difference between them. Similar observations were made by Gustafsson (1948) on the flora of the most severe alpine regions of the Scandinavian mountains, with comparable results. At the same time several workers showed that artificially produced autopolyploids of several species (Stebbins 1950, Tal 1980) are not more and may be less resistant to frost than are their diploid progenitors. These investigations indicated that the correlation observed by Tischler and others might be explained in a different way.

An alternative interpretation was suggested by Reese and the present author (Stebbins 1950). The cool, temperate and arctic regions of Europe and eastern North America, from which most of Tischler's counts were obtained, were heavily covered by the Pleistocene ice sheets. After they had retreated, vast areas were open to colonization on the part of plants that were adapted to the radically new conditions that resulted from the action of the glaciers themselves and of fluvial activity in periglacial regions. Polyploidy, particularly when it is accompanied by hybridization between either different species or different ecotypes of the same species, is the quickest way possible by which new species or races can evolve that are adapted to new ecological conditions. Hence the high frequency of polyploids in most regions of high latitude in the northern hemisphere could have been brought about by polyploid evolution during the several advances and retreats of ice sheets. The final advance of plants into the regions laid bare by the retreat of the most recent ice sheets (Würm or Wisconsin), could be regarded as having been achieved both by polyploids that arose after earlier glaciations, and by those that evolved immediately prior to the time when present habitats opened up.

Still another hypothesis for the origin of arctic polyploids was advanced by Sokolovakaya and Strelkova (1940, 1960; Sokolovskaya 1963). They postulate that ancestral diploids of the genera concerned existed chiefly at high altitudes at lower latitudes: Alps, Caucasus, Central Asia, Altai, Rocky Mountains. As the arctic climates ameliorated sufficiently to permit colonization by angiosperms, polyploid races and species generated in these mountains migrated northward to colonize the newly available areas.

Another hypothesis concerning the origin of the modern arctic flora, that does not take into account the phenomenon of polyploidy, is that of Hultén (1937, 1968), who postulated that extensive unglaciated refuges, both in eastern Siberia and the northern half of Alaska, contained many of the ancestors of the modern flora. He suggested that much of the post Pleistocene migration was not from south to north, but eastward and westward from the Beringian refuge. The three principal hypotheses can be designated and summarized as follows.

1. *The increased hardiness hypothesis.* (Tischler, see Stebbins 1950). Diploid ancestors of arctic and alpine polyploids existed at lower latitudes, and chiefly at lower altitudes. As mountain ranges became higher, and the northern climates became more severe, mutations to polyploidy brought with them greater resistance to the more severe conditions, and thus permitted the polyploids to occupy the newly available regions of higher altitude and latitude.

2. *The alpine-arctic migration hypothesis.* The genera that now form the arctic flora evolved resistance to severe conditions before the Pleistocene glaciations, in adaptation to the alpine conditions produced by the rise of mountain ranges during the Pliocene

epoch. Although polyploidy may have been involved, most of the newly formed alpine species were diploids. Polyploids were generated and spread northward as regions became opened up by the retreat of the Pleistocene glaciers.

3. *The secondary contact hypothesis.* This hypothesis, presented here for the first time, is an outgrowth of the hypothesis that polyploidy, accompanied by hybridization, is instrumental chiefly for rapid adaptation to new ecological conditions that become available relatively suddenly. During the latter half of the Pliocene and beginning of the Pleistocene epochs, a period of 5–6 million years, many plant genera responded to the increasingly harsh conditions along the crests of the newly rising mountain ranges as well as at higher latitudes by evolving races and species, chiefly diploid, having increased tolerance of cold, and in the north, of the long arctic nights. With the onset of the Pleistocene glaciations, alpine populations colonized lower altitudes and northern populations moved southward. Many secondary contacts between different radiants were repeatedly established and broken. Hybridization between previously separated populations, accompanied or followed by either polyploidy or introgression at diploid levels, generated new races and species, some of which became adapted to the new conditions prevailing in regions vacated by the ice. These new races and species, that now form the bulk of the arctic-alpine flora, originated during the entire period of a million years or more during which glaciers advanced and retreated, but some of them probably date from the beginning of the final recession, about 10,000 to 14,000 years ago.

The point must be repeatedly emphasized that this hypothesis does *not* imply that polyploid species and races inhabiting arctic-alpine regions are exclusively allopolyploids. As I have stated in several publications (Stebbins 1950, 1971, 1980), polyploidy plays an important role in genetic stabilization of favorable new gene combinations derived from hybridization between interfertile races that have different adaptive norms. Moreover, many hybrid polyploids, known as segmental allopolyploids, form a complete spectrum of conditions intermediate between auto- and allopolyploidy. The majority of arctic-alpine polyploids may well belong in this latter category.

Predictions and observations that test three hypotheses

The first hypotheses about the origin of arctic-alpine polyploids were based upon comparisons between the frequency of diploids and polyploids in the entire flora of different regions. The weaknesses of this method, mentioned in the introduction, can now be partly overcome. For many floras, chromosome numbers are available for species collected in the region concerned, and many widespread species are known for so many different regions that one can decide with reasonable probability whether or not they include races having different ploidy levels. Moreover, biased results due to mixing indiscriminately species having different growth habits can be eliminated by comparing separately woody groups, perennial herbs and annuals. The latter are so few as indigenous components of indigenous arctic-alpine floras that they can be disregarded. With these precautions in mind, floras were compared of regions in which the chromosome numbers are known for 70 per cent or more of the species.

The following prediction can be made. If the increased hardiness hypothesis is correct, a good correlation should exist between harshness of climate and percentage of polyploidy. There should be no examples of decreasing frequency of polyploids as one progresses northward from a milder to a harsher climate.

The flora of Alaska effectively refutes the above prediction. Southern Alaska has, for its latitude, a relatively mild, oceanic climate. Minimal temperatures for the coldest

month are Sitka -6°C and for Anchorage -14.7°C . Precipitation is abundant: from 800 to 4000 mm. Central and northern Alaska have a much harsher climate. Minimal monthly temperatures are for Fairbanks -30°C , for Nome -25°C , and for Point Barrow -31°C . Precipitation is light to scanty, from 400 mm down to 100 mm.

Chromosome numbers for the flora were compiled from the encyclopedia edited by Fedorov (1969), and from recent publications dealing with Alaska itself (Johnson and Packer 1968, Packer and McPherson 1974, Dawe and Murray 1979, 1980, 1981). Tab. 1 summarizes the results. It compares the frequencies among those species that, according to range descriptions and maps contained in the two floras (Hultén 1968, Welsh 1974), occur chiefly in the southern half and in the central and northern part of the state.

This comparison shows that percentages of polyploidy are somewhat lower in the central and northern regions that have relatively harsh climates. They support the evidence from floras of the high Alps and the Scandinavian mountains (Favarger 1954, Gustafsson 1948), as well as physiological data on autopolyploids mentioned above. The flora of the Queen Charlotte Islands, British Columbia, that is south of the southern tip of Alaska, has an even higher frequency of polyploids. The increased hardiness hypothesis, now fully refuted, is not considered further.

By themselves, the Alaskan data do not permit discrimination between the alpine-arctic migration and secondary contact hypotheses. Nevertheless they favor the latter hypothesis, since southern Alaska and the Charlotte Islands were extensively glaciated, while central and northern Alaska contain extensive refuges not covered by the Wisconsin (Würm) ice sheet, including the Fairbanks and Nome areas, as well as Ogotoruk Creek, of which the flora is also tabulated in Tab. 1.

There are two reasons for this. In the first place, the northern floras contain an appreciable number of diploid species: 50.2 per cent at Ogotoruk Creek and 30 out of 68 species that were collected at the extreme northern station of Point Barrow. Such high percentages do not favor the hypothesis that most polyploids were generated in alpine areas and migrated northward. Secondly, the fact that both with respect to the flora as a whole and separate local florulas, somewhat higher percentages are recorded for the southern half of Alaska can be explained by assuming that the polyploids were somewhat better invaders of the heavily glaciated regions in the southern half. If that explanation is valid, then among floras of similar latitudes, having different amounts of glaciation there should be a correlation between the percentage of polyploidy and the extent to which the region was glaciated.

Tab. 1. *Percentage of polyploidy in angiosperm floras of the North Pacific Basin*

Region	Latitude	# SPP	% sample	% polyploidy total	Perennial herbs	Source
Marin County U.S.A.	38°	585	69	33.7	41.9	original
Queen Charlotte Ids. B.C.	52–54°	–	–	56.0	58.2	Taylor, Mulligan 1968
Southern Alaska	55–63°	482	79	50.2	53.7	original
Northern Alaska	63–71°	420	82	47.9	50.7	original
Ogotoruk Valley, Alaska	68°	233	80	49.8	51.7	Johnson, Packer 1968
Eastern Siberia, USSR	64–73°	382	–	55.0	59.0	Zhukova 1965a, b, 1960, 1967, 1968, 1969

Tab. 2. *Percentage of polyploidy in angiosperm floras of the North Atlantic Basin*

Region	Latitude	# SPP	% sample	% Poly-ploidy total	Perennial herbs	Source
Slovenia	46°	2350	95	39.5	42.5	Löve and Löve 1974
Mt. Desert. Me.	44°	354	81	44.6	47.8	original
Western Alps	46–47°	–	–	43.1	–	Favarger 1961
Britain	50–58°	1114	88	46.7	51.4	Clapham et al. 1962
Iceland	63–66°	290	90	61.0	61.5	Löve and Löve 1956
Greenland	60–75°	337	93	64.4	68.7	Böcher et al. 1968

This prediction is tested by comparing the flora of Alaska with those of Iceland, that was almost completely glaciated, and Greenland, where some nunataks may have provided refuges (Tab. 2). If the secondary contact hypothesis is valid, glaciated regions that are also insular, and therefore subjected to immigration during interglacial and particularly postglacial periods, should have higher percentages than continental regions. The higher percentages in Greenland and Iceland as compared to other glaciated regions such as Britain, the eastern United States (Mt. Desert) and the western Alps, could be explained upon this basis. This explanation is reinforced by the data in Tab. 2 on floras of middle latitudes (44–60°). Among them, the highest percentage of polyploidy is on the Queen Charlotte Islands, that are not only themselves an archipelago, but are part of an extensive archipelago that extends all the way from Southern Alaska to Puget Sound, in the state of Washington. Throughout this area, repeated advances and retreats of the ice sheets made possible a large number of secondary contacts between populations. Southern Alaska, part of which forms the northern section of this archipelago, to which is added that of the Aleutian Islands, had a similar history, and a percentage of polyploidy that is only slightly lower. Britain, that is insular but intimately connected with the European Continent, has intermediate values. The lowest values among floras that occupy predominantly glaciated areas are those of the coast of Maine and the Western Alps, both of them continental. The lowest values are, as expected in Slovenia and northern California, both of them continental and little or not at all affected by Pleistocene glaciation. The great differences in percentage of polyploidy in Marin County between the flora as a whole (33.7) and perennial herbs (42.5) is due to the presence of a high proportion of angiospermous shrubs and of annuals. The percentages for these life forms are 13.5% for the woody species and 20.8% for the annuals. These data emphasize the need for making comparisons only between plants having similar growth habits.

The high values for the Chukotsk Peninsula and neighboring regions of eastern Siberia are somewhat surprising, since this region is continental and was only partly glaciated. It might be explained by the fact that during the height of the Pleistocene glaciation it was a mosaic of glaciated and non-glaciated areas (Petkov 1967).

Distribution of diploids and polyploids in particular genera and species complexes

A better way of comparing the probability of the alpine-arctic migration and secondary contact hypotheses is on the basis of the differential distribution of diploids and polyploids within individual genera and species complexes. The following examples include the majority of genera of the arctic flora within which polyploid series exist. Eight of them are discussed individually: the remainder are summarized in Tab. 4.

Calamagrostis. A large enough number of species of this grass genus have been counted so that its basic number can be regarded as $x = 14$: a secondary derivative of the number $x = 7$, that is characteristic of related genera. Diploid ($2n = 28$) species that do not contain polyploid races are widespread in southern and central regions of its areal distribution in both the Old and New Worlds. The arctic species are chiefly races of *C. canadensis*, *inexpansa-neglecta*, *lapponica*, *purpurascens*, and *purpurea*. Each of these complexes contains diploid ($2n = 28$) races in the far north, and for most of them either diploid races or closely related species are found at or near the southern border of the range of the genus. In the far north, diploid races of *C. neglecta* and the related *C. Holmii* are widespread (Zhukova 1967, Nygren 1958); those of *C. lapponica* are reported by Sokolovskaya and Strelkova (1960) and Bowden (1960) and by Johnson and Packer (1968); and of *C. purpurea* by Sorsa (1962) and Zhukova (1967). The polyploid races of all of these species complexes are chiefly apomictic (Nygren 1946, 1954). They are most abundant in lowland cool temperate and subarctic glaciated regions. *Calamagrostis*, therefore, fulfills well the predictions of the secondary contact hypothesis.

The Campanula rotundifolia complex. The distribution of diploids and tetraploids in this complex is well summarized by Böcher (1960). He reports diploids from northern Greenland, Spitzbergen, and various, mostly restricted areas in central and southern Europe. Additional more recent counts for related species endemic to low and middle altitudes of southern Europe are reported in the Flora Europea (Tutin et al. 1976). The common races throughout central Europe and all those native to North American are tetraploid. The secondary contact hypothesis is well fulfilled.

Chamaenerion. This genus, sometimes regarded as a section of *Epilobium*, has been discussed by Mosquin (1967) and Small (1968) (Mosquin and Small 1971). The diploid race of its most widespread species, *E. angustifolium*, is predominant in Eurasia and in North America and extends from arctic regions to northern Canada. Diploid *E. latifolium* extends from northwestern Alaska (Johnson and Packer 1968) to Colorado. Tetraploid *E. angustifolium* is found in the northern United States and southern Canada while tetraploid *E. latifolium* extends from Central Alaska (Dawe and Murray 1981) to the Rocky Mountains of Montana. Although Small believes that hybridization between the two species has not played a role in their evolution, Böcher (1962) has documented hybrids between them, and many herbarium specimens of presumably tetraploid *E. latifolium* have leaves that are narrower than those of its diploid races, thus approaching *E. angustifolium* in one of the most distinctive characteristics that separate the two species. More data are needed before the presence or absence of hybridization can be determined with certainty. If effective hybridization can be documented, the genus is an excellent support for the secondary contact hypothesis. Since most of its races are adapted to lowlands, it does not in any way support the alpine-arctic migration hypothesis.

Geum and its relatives. Based largely upon the careful investigations of Gajewski (1959), nearly all species of *Geum*, s.str. have long been known to form a polyploid series on the basic number $x = 7$, but even though nearly all of its species have been investigated, none is known to be diploid ($2n=14$). More recently, however, two diploid species have been recorded for the genus *Sieversia* (*S. pentapetala*, *S. pusilla*) that many authors include within *Geum* (Sokolovskaya 1963, Zhukova 1966). Both species occur in unglaciated north temperate eastern Asia; *S. pusilla* extends into arctic Siberia in the Kolyma area. Although no other diploid species are known that belong to *Geum* even in the broadest sense, Gajewski has pointed out its close relationship to *Waldsteinia* and *Coluria*, both of which contain diploid temperate forest loving species that have

ecological adaptations not unlike those of the more southerly species of *Geum* s.str. The latter genus may therefore have resulted from allopolyploidy involving ancestral species of *Sieversia* and of *Waldsteinia*, *Coluria* or an extinct genus related to them. At any rate, there is no evidence to indicate that the widespread species of the *Sieversia* affinity, placed by some botanists in *Sieversia*, *Neosieversia* and *Acomastylis*, are even partly descended from diploids adapted to higher mountains of intermediate latitudes, since no such diploid species are known.

Puccinellia. This genus is confined to saline or brackish moist habitats, mostly along temperate to arctic seacoast, but with a few inland species found in brackish or alkaline depressions. Four of its diploid species, *P. colpodoides*, *P. Langeana*, *P. poacea* and *P. Wrightii* are distributed in arctic regions, while two, *P. lemmonii* and *P. Parishii*, occupy alkaline depressions in west central United States. A seventh diploid, the arctic species sometimes recognized as *P. Vahliana*, is by other authors included in the neighboring genus *Colpodium*. The origin of *Puccinellia* polyploids from montane or high alpine diploids is highly improbable, but relatives of its existing diploids may well have been in contact with each other during the successive advances and retreats of Pleistocene glaciers.

The genus Pulsatilla. Sometimes recognized as a subgenus of *Anemone*, this genus of 18 species contains diploids and tetraploids. Diploid *P. patens* extends northward to arctic Alaska, and Siberia, while diploids of several species occur at or near the southern limit of the genus. Tetraploids are most frequent in intermediate latitudes, such as central and western Europe. Their origin is best explained by the secondary contact hypothesis.

The arctic species of *Salix*. Among the most characteristic features of Arctic tundra and, to a lesser extent, some alpine regions at lower latitudes, are dwarf willows. According to Argus (1973) and other authors, at least 16 diploid species are found in or extend into arctic regions. Hence, the origin of such widespread arctic polyploid species as *S. arctica*, *S. arctophila*, *S. glauca* and *S. polaris* is best explained as a result of repeated secondary contact between some of these species, that resulted in hybrid polyploidy.

The genus Saxifraga. This is one of the largest and most complex genera that is characteristic of arctic-alpine regions. At present, distribution patterns of cytotypes in the numerous species that possess different chromosome numbers are poorly known (Johnson and Packer 1968). Here I compare only the overall distribution pattern in species having chromosome numbers at three levels: probably diploid (12–22), diploid with respect to near relatives, but perhaps of ancient polyploid derivation ($2n = 24–28$); and most probably polyploids of more recent derivation ($2n = 30–112$). The tabulation presented in Tab. 3 shows two trends. First, with increasing chromosome numbers, the proportion of species that occupy arctic-alpine regions decreases at the expense of an increasing proportion of species adapted to temperate regions. Second, in all of the three levels of chromosome number, alpine species that do not extend into the arctic form the smallest category. This suggests that the genus may have evolved first at higher latitudes, and that both the temperate species and those that occupy alpine habitats at lower latitudes are mostly derived.

Genera that are less well known. Tab. 4 presents a few preliminary data on most of the remaining genera of the arctic flora, which are even more poorly known than those discussed above. Its object is to show what proportion of them are completely lacking in diploids that have reached arctic regions. This proportion is small; only five out of the 36 listed. All five of them, moreover, are such that their distribution patterns mean

Tab. 3. *Latitudinal distribution of diploid chromosome numbers of species and cytotypes in Saxifraga*

Distribution pattern	Numbers of entities having diploid chromosome numbers		
	12–22	24–28	30–112
Arctic or arctic-alpine	8	11	9
Alpine, middle latitudes	6	10	6
Temperate	7	24	26

little, at least on the basis of present knowledge. In *Agropyron*, as used in the source of the data (Fedorov 1969), the species are mostly allopolyploids of which at least one parent is related to either *Hordeum* or *Elymus*, s. lat. (Dewey 1982). The arctic species are by some authors placed in the genera *Roegneria* and *Elytrigia*. Nevertheless, it is true that no diploids of any of these genera are now present in the arctic. This complex is a good candidate for the alpine-arctic migration hypothesis. Another such candidate is *Taraxacum*, of which all of the known arctic microspecies are apomictic polyploids. Their relatives are in the high mountains of Central Asia.

With respect to the other genera in this category, only one diploid is known in *Hierochloe*: *H. australis* of Central Europe. This genus, also, probably migrated northward after polyploids had originated at lower latitudes. The genera *Juncus* and *Senecio* are chromosomally anomalous. The great majority of their perennial species are tetraploid as compared to a small group of annuals: In *Juncus* the only known diploid species is a tiny annual, *J. capitatus*. A few species of *Senecio* have $2n = 10$, which

Tab. 4. *Distribution patterns of circumpolar or bicontinental arctic or arctic-alpine diploids*

3–5 circumpolar diploids	2 circumpolar diploids	1 circumpolar diploid	Endemic arctic-alpines, both hemispheres
<i>Artemisia</i>	<i>Androsace</i>	<i>Alopecurus</i>	
<i>Potentilla</i>	<i>Arenaria</i> *	<i>Antennaria</i>	<i>Arabis</i>
<i>Primula</i>	<i>Aster</i>	<i>Cardamine</i>	<i>Gentiana</i> (?)
<i>Ranunculus</i>	<i>Astragalus</i>	<i>Castilleja</i>	<i>Papaver</i>
	<i>Draba</i>	<i>Cerastium</i>	
	<i>Potamogeton</i>	<i>Festuca</i>	
		<i>Gentianella</i>	
		<i>Lychnis</i>	
		<i>Oxytropis</i>	
		<i>Poa</i>	
		<i>Polygonum</i>	
Arctic-alpine diploids, OW only	A-A diploids, NW only	No A-A diploids	
<i>Agrostis</i>	<i>Arnica</i>	<i>Agropyron</i>	
<i>Elymus</i>	<i>Erigeron</i>	<i>Hierochloe</i>	
<i>Euphrasia</i>		<i>Juncus</i>	
<i>Luzula</i>		<i>Senecio</i>	
		<i>Taraxacum</i>	

* Includes *Minuartia* and *Moehringia*

suggests that its original basic number may have been $x = 5$. The species having $2n = 20$ or tetraploid, if that supposition is correct, are also relatively few in number, and none of them is either alpine or arctic in distribution. Even among those having $2n = 40$ or $2n = 43$, species adapted to temperate climates far exceed the arctic-alpine species, and only a few scattered species of cytotypes have arctic or alpine distributions. In *Senecio*, adaptation to arctic-alpine conditions took place without a change in chromosome number, at a ploidy level which was either tetraploid or octoploid, depending upon one's interpretation of the species having $2n = 10$.

Another problem genus is *Gentiana*. The majority of its species: 42 out of 66, have either $2n = 26$ or $2n = 36$; numbers that are not multiples of each other. They would be difficult to place in the same polyploid series. The latter number could be regarded as tetraploid on the base $x = 9$. A single diploid on this base, *G. tornezyana* has been found in the high mountains of Africa. The number $2n = 26$ might be a modified tetraploid level on $x = 7$, since a single species having $2n = 14$, *G. nivalis* is in the Alps and other mountains of central Europe. (Refs. in Fedorov 1969). No species are known having $2n = 12$, although both $2n = 10$ and $2n = 14$ are known. The number $2n = 24$, found in the arctic *G. glauca*, may be a tetraploid based upon the missing $2n = 12$, or an allopolyploid of $2n = 10$ and $2n = 14$. Since hardly more than one-fifth of its 300 species have been counted, further research in this genus may reveal a meaningful and highly interesting pattern.

In the remaining 29 genera listed in Tab. 4, most species form a simple polyploid series based upon a single haploid or x number. In all of them, at least one diploid is found in arctic regions, and in nearly all of them two or more such species are known. Hence, a good case can be made for the hypothesis that the arctic regions were colonized largely by diploids, and that most of the polyploids that are found there now were evolved from diploids that were already adapted to the arctic habitat.

General discussion

Ages of polyploids. As many authors have pointed out (Stebbins 1950, 1980, Favarger 1967), polyploids may be either very recent, middle aged, or ancient. This gradation holds for at least some members of the arctic-alpine flora. Because of the difficulty of assigning ages, this author cannot accept Favarger's (1961) classification into paleopolyploids, mesopolyploids and neopolyploids. One of his criteria, the amount of morphological difference between the polyploid and its nearest known diploid ancestor, would be valid only if nearly all natural polyploids were autopolyploids that had diverged from their ancestor due to mutation, an hypothesis which this author cannot accept, for reasons discussed elsewhere (Stebbins 1971, 1980). In the present treatment, species or cytotypes have been classified as diploid either if no lower number is known in the genus, or if such lower numbers cannot be regarded as potential diploid ancestors. The difficulties even of this method are discussed above, with reference to *Juncus*, *Senecio* and *Gentiana*.

The general application of the secondary contact hypothesis. The secondary contact hypothesis applies not only to the arctic-alpine hypothesis, but to polyploidy in general. As emphasized above and in earlier publications, strict autopolyploids derived from a single diploid population, can have local success, but for various reasons are unlikely to spread far beyond the distributional range of their diploid ancestor. Widespread polyploids are almost all of hybrid origin, most often resulting from contacts between

different ecotypes of the same species, between closely related diploid species, or between a polyploid, its ancestor, or a closely related diploid. Consequently, a rough correlation can be expected between frequency and degree of polyploidy and the number of secondary contacts between related populations that have occurred in the recent past. One line of evidence in favor of this hypothesis comes from comparisons between closely related genera, between sections or subgenera of the same genus, and between regional areas of the same genus that have been subject to different geological histories. The hypothesis would predict that genera having highly patchy distributions, so that separation and reunion of populations through time periods as recorded in the geological time scale would often produce separation and reunion of populations, would have high frequencies of polyploidy. The same would be expected of populations inhabiting archipelagoes or isolated mountain summits. On the other hand, species or genera adapted to widespread, homogenous forest belts, or to stream banks that provide continuous linear habitats, would have low frequencies.

A few examples show that this prediction is often fulfilled. In the Salicaceae, *Populus* species inhabit chiefly stream banks, while those of *Salix* occupy either stream banks, mountain slopes, boggy meadows or tundra. As expected, polyploidy is virtually lacking in *Populus*, but is highly developed in some sections of *Salix*. A similar difference exists in the Betulaceae. *Carpinus*, *Corylus* and *Ostrya* that inhabit stream banks or homogeneous forests, are virtually devoid of polyploids; *Betula*, of which most species occupy montane, subarctic forests or arctic bogs, contains many polyploids, while *Alnus* is intermediate in both respects. In the large genus *Rhododendron*, polyploidy is virtually absent except in the region of eastern Asia that contains a series of high, closely adjacent mountain ranges (Janaki-Ammal, in Favarger 1961). In most genera of Ericaceae polyploidy is rare or absent, but in *Vaccinium*, which occupies a variety of localized habitats, it is highly developed. Several other examples could be cited.

History of the arctic-alpine flora. The history of any flora is difficult to decipher, particularly when, as in the arctic flora, much of the territory that is originally occupied either was repeatedly denuded of plants and recently reoccupied, or as in the case of Greenland, Baffinland and Scandinavia, contains regions that are still ice covered. For such examples one must resort to logical deduction as well as direct evidence.

As Johnson and Packer (1967) have emphasized, the differentiation of an arctic-alpine biota began during the Tertiary Period, at least as early as the middle of the Pliocene Epoch, and perhaps even in late Miocene times. Pollen records of Tertiary localities at high latitudes are only from relatively southern lowlands, so that the predominance of forest floras in these areas says nothing about events that were taking place at higher latitudes and altitudes. My deduction is that the areas which now exhibit the most extreme arctic-alpine conditions were the first ones in which plants adapted to them evolved. Before Greenland was covered by its gigantic ice cap, it must have presented highly favorable conditions for the evolution of an arctic-alpine flora, a condition that may have existed in smaller arctic islands, such as Baffinland, Ellesmere Land, Spitzbergen and Novaya Zemlya. I believe that these regions formed the cradle of the arctic-alpine flora, from which plants migrated before the ice caps were completely formed. The original flora became extinct except for relictual species that still survive in marginal refuges. Migrations from these centers could have been eastward, westward or southward. During the latter half of the Pliocene and through most of the Pleistocene, similar floras must have evolved in high mountain ranges of temperate latitudes, such as the Scandinavian mountains, Alps, Caucasus, Central Asia and Altai

in the Old World, and the Rocky Mountain system in the New World. The ancestors of these strictly alpine floras could have been either migrants from lower altitudes or descendants of early colonists from the north. Consequently, directions of migration could have been either eastward, westward, southward or northward. With the climatic fluctuations that were already evident toward the end of the Pliocene and have continued throughout the Pleistocene to the present, secondary contacts between segments of arctic-alpine floras were innumerable, and were often being established and broken.

Although many of the arctic-alpine genera are far too poorly known so that past directions of migration can even be hypothesized for them, at least some examples can be established with a reasonably high degree of probability for each of the directions of migration postulated above.

1. Migrations chiefly eastward and westward at high latitudes, southward only during glacial maxima. *Phippsia*, *Dupontia*, *Colpodium*.
2. Migrations circumpolar, northward in the New World, plus southward in the Old World (Temperate diploids few or lacking in Old World). *Erigeron*, *Arnica*, *Polemonium*.
3. Migrations northward in the Old World, circumpolar, southward in the New World (Temperate diploids few or lacking in New World). *Agrostis*, *Alopecurus*, *Androsace*, *Armeria*, *Chamaenerion*, *Eritrichium*, *Euphrasia*, *Hierochloa*, *Lychnis*, *Myosotis*, *Papaver*, *Phleum*, *Primula*, *Saussurea*, *Silene*, *Taraxacum*.
4. Migrations circumpolar, southward in both hemispheres: *Dryas*, *Koenigia*, *Luzula*, *Oxyria*, *Oxytropis*, *Parnassia*, *Puccinellia*, *Pulsatilla*.
5. Migrations northward in Old World, little circumpolar and no New World southward migrations. *Bupleurum*, *Cochlearia*, *Dianthus*, *Dracocephalum*, *Lagotis*.
6. Migrations northward in New World, little circumpolar, no southward migrations in Old World. *Castilleja*, *Lesquerella*, *Mertensia*, *Phyllodoce*, *Zygadenus*.

The larger genera, such as *Festuca*, *Poa*, *Calamagrostis*, *Salix*, *Draba*, *Ranunculus*, *Saxifraga*, *Potentilla*, *Astragalus*, *Artemisia* and *Senecio*, have such complex patterns that much more needs to be known about them before directions of migration can even be postulated. Most probably, the majority of them include sections or species groups having very different migration patterns. Clearly, no absolute rules or generalizations can be made about migration patterns of the arctic-alpine flora.

Ecological considerations and prospects for the future. The most recent discussions of polyploidy and arctic-alpine floras, particularly those of Favarger (1961) as well as Johnson and Packer (1965, 1967, 1968) have emphasized increasingly the importance of ecological factors in determining relative distribution patterns of diploids and polyploids. This type of evidence is proving to be the most valuable of all. It needs to be extended from statistical comparisons of plant associations to studies in depth of individual genera, species groups, and particularly taxonomic species having different cytotypes. The focus needs to be upon the relative importance of change in chromosome number as compared to genetic mutation and hybridization. New techniques, such as cladistics, computerized comparisons of associations, and in particular comparisons of secondary plant products, proteins, and DNA sequences of ribosomal nuclear DNA, mitochondrial and chloroplast DNA, are now available for comparisons between closely related species as well as different races of the same species. Syntheses that could result from combined attacks upon the same group from all of these directions are likely to lift arctic-alpine evolutionary research to a new level, and to enable this kind of research to make major contributions to general problems of evolution.

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