

POLYPLOIDY AND GEOGRAPHIC DISTRIBUTION IN SPIRAEA

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THE GENUS *Spiraea* is widely distributed in both the Old and New Worlds, although the center of distribution appears to be in Asia, where the genus is best represented. Polyploidy — both autopolyploidy and allopolyploidy — is a common feature in other members of the Rosaceae, and *Spiraea* is no exception in this respect. Many species appear to cross readily, which adds to the complexity of the genus.

Some cytological work has been done with *Spiraea* in connection with chromosome relationships in the Rosaceae and especially in relation to the origin of the Pomoideae (Sax 1932). The genus is not favorable for cytological work; the anthers are very small at the time of meiosis, the chromosomes are small and are differentiated from cytoplasmic inclusions with difficulty. The flowering period for the genus extends from April to July, so that collections must be made over a period of several months.

Chromosome counts were determined from aceto-carminic smear preparations. Pollen fertility was determined for various species and species hybrids, and the date of flowering was recorded. The basic chromosome number is 9, and not 8, as previously reported. In many cases it was difficult to determine the exact number of chromosomes, especially in some of the polyploids and species hybrids. The data obtained from the various species are recorded in Table I.

Most of the species of the first section of the genus are diploids with 9 pairs of chromosomes at meiosis. The two exceptions appear to be autopolyploids. *Spiraea myrtilloides*, a hexaploid, is similar to *S. gemmata*, and may be an autopolyploid form of the latter species, even though it is somewhat smaller. The other exception is clearly an autopolyploid of *S. chamaedryfolia*, giving rise to the variety *ulmifolia*. The variety is larger and has a greater distribution than the type, and tends to reproduce vegetatively by suckers. All species examined in the section Chamaedryon are relatively fertile. All are natives of the Old World and all are early-flowering.

Only three species in the section Calospira were studied. *Spiraea Miyabei* is an early-flowering diploid but is relatively sterile. Both the

TABLE I
SPECIES OF SPIRAEA

Species	Chromosome number	Pollen fertility	Date of flowering	Habitat
Sect. I				
<i>prunifolia</i>	2n	96%	May 1	O ¹
<i>Thunbergii</i>	2n	80%	May 1	O
<i>hypericifolia</i>	2n	70%	May 8	O
<i>nipponica</i>	2n	95%	May 28	O
<i>gemmata</i>	2n	94%	May 13	O
<i>mollifolia</i>	2n	81%	May 13	O
<i>myrtilloides</i>	6n	85%	May 20	O
<i>cana</i>	2n	97%	May 25	O
<i>media</i>	2n	60%	May 20	O
<i>chamaedryfolia</i>	2n	86%	May 13	O
— <i>ulmifolia</i>	4n	80%	May 20	O
<i>pubescens</i>	2n	75%	May 20	O
Sect. II				
<i>Miyabei</i>	2n	8%	May 1	O
<i>japonica</i>	2n	98%	June 26	O
<i>corymbosa</i>	3n	0	June 15	N ²
Sect. III				
<i>salicifolia</i>	4n	1%	July 2	O
<i>alba</i>	4n	99%	July 7	N
<i>latifolia</i>	4n	95%	July 2	N
<i>Douglasii</i>	4n	95%	July 2	N

good and imperfect pollen grains remain in tetrads at the time of flowering. Sterility appears to be caused by some general physiological factor, because there is little irregularity in meiosis, and all pollen grains in a given tetrad are either good or imperfect. This sterility can not be attributed to chromosome irregularities or to segregation of genetic factors. *Spiraea japonica* is the only late-flowering species which is known to be a diploid. The American species, *S. corymbosa*, is a triploid with complete pollen sterility. It must form viable egg cells or exist in a fertile diploid form, because it is involved in certain species hybrids.

¹Old World.

²New World.

All the species listed in the section *Spiraria* are tetraploids. These are late-blooming forms and, with the exception of *S. salicifolia*, they are highly fertile. Most of the species in this section are natives of North America. Two other American species, *S. Menziesii* and *S. tomentosa*, were available in the Arnold Arboretum, but we were unable to obtain chromosome counts. The flowers, at the time of meiosis, are very small, and the anthers are minute.

There are many species hybrids of *Spiraea* which have originated in nature or in cultivation. The chromosome number and pollen fertility have been determined for nine of these hybrids (Table II).

TABLE II
SPIRAEA SPECIES HYBRIDS

Hybrid	Chromosome number	Pollen fertility	Parent Habitat
<i>pikoviensis</i> (<i>crenata</i> × <i>media</i>)	4n	94%	O×O
<i>inflexa</i> (<i>crenata</i> × <i>cana</i>)	2n	95%	O×O
<i>pachystachys</i> (<i>corymbosa</i> × <i>Douglasii</i>)	3n	5%	N×N
<i>blanda</i> (<i>chinensis</i> × <i>cantonensis</i>)	2n	42%	O×O
<i>Billiardii</i> (<i>Douglasii</i> × <i>salicifolia</i>)	5 or 6n	1%	O×N
<i>notha</i> (<i>corymbosa</i> × <i>latifolia</i>)	4n	13%	N×N
<i>Margaritae</i> (<i>japonica</i> × (<i>albiflora</i> × <i>corymbosa</i>))	2 and 4n	0	O×N
<i>cinerea superhypericifolia</i> (<i>hypericifolia</i> × <i>cana</i>)	2n	65%	O×O
<i>intermedia</i> (<i>albiflora</i> × <i>Douglasii</i>)	4n	0	O×N

Two of the species hybrids, *S. pikoviensis* and *S. inflexa*, are highly fertile, and both involve Old World species in the first section of the genus. The parental species, *S. media* and *S. cana*, are known to be diploids, and since the hybrid, *S. inflexa*, is a diploid, the species *S. crenata* probably is a diploid. The hybrid *S. pikoviensis* is a tetraploid, apparently of allopolyploid origin.

Crosses between species in the first section also produce hybrids which are partially sterile. *Spiraea blanda* is a cross between the diploid species *S. chinensis* and *S. cantoniensis*. There is some irregularity in chromosome pairing at meiosis, and less than half of the pollen is good. The hybrid *S. cinerea superhypericifolia* is a hybrid segregate showing about 65 per cent fertility.

Several hybrids, *S. pachystachys*, *S. Billiardii*, *S. notha*, and *S. Margaritae*, are derived from either *S. corymbosa* or *S. salicifolia* as one of the parents. These two species, as represented in our collection, have little or no perfect pollen, and must have viable egg cells or include strains

which are more normal in fertility, in order to hybridize. The hybrids involving these parental species are highly sterile, even when both parents belong to the same section. It seems probable that the pollen-sterile parents have some viable egg cells but carry genetic factors for pollen sterility.

The hybrid *S. Billiardii* was produced by crossing two tetraploids, but the hybrid has more than $4n$ chromosomes and probably is a hexaploid. Apparently unreduced gametes were produced by one of the parental species. Confirmation of such behavior in *Spiraea* is found in the hybrid *S. Margaritae*, a backcross involving three species. In this hybrid both diploid and tetraploid pollen mother cells were observed in flowers from the same plant, but the divisions were somewhat irregular, and no good pollen was formed. In several species there were occasional microsporocytes with twice the normal chromosome number. Whether these were isolated tetraploid areas or the result of asynapsis could not be determined.

The relations between geographic distribution, polyploidy, and time of flowering are very marked in *Spiraea*. Most of the Old World species are early-flowering diploids, while all American species are late-flowering; and of those examined cytologically, all are tetraploids. Tetraploidy alone is not responsible for the delay in time of flowering, because the tetraploid variety of *S. chamaedryfolia* is little later than the diploid parent, and the only hexaploid species found is relatively early in flowering. In general, however, the polyploid forms in most genera flower later and over a longer period than the diploids (Müntzing 1936).

The greater vigor, hardiness, and adaptability of polyploids result in the extension of the range of certain genera (Tischler 1935, Müntzing 1936, Anderson and Sax 1936). The polyploids are more frequently found at the periphery of the range. In those genera of Old World origin which are also represented in North America, one might expect a greater proportion of polyploids in the New World. Such a relation is found in *Spiraea* and in certain other genera of the Rosaceae. In *Malus*, for example, most of the oriental species are diploids, while most of the American species are tetraploids. The oriental species flower earlier than the native species and, in the Arnold Arboretum, the flowering periods of the two groups do not overlap. There is somewhat more polyploidy in the native American species of *Rosa* than in the Old World forms, but in *Prunus* there seems to be no such relationship. A comparison of species in certain genera may not be reliable because so many species used for cytological work have been in cultivation for

many generations, and selection in cultivated forms is more likely to perpetuate polyploid variants (Anderson and Sax 1936). Most of the spiraeas in our collection are of recent introduction, and with the exception of some of the hybrids, their behavior should be comparable with those found in nature. Although there is a rather striking relationship between polyploidy, time of flowering, and geographic distribution in *Spiraea* and *Malus*, there are many genera of Asiatic origin which show no such relationships between the Old and New World species.

SUMMARY

The basic chromosome number for *Spiraea* is 9. Most of the Old World species are early-flowering diploids, while the American species studied are late-flowering tetraploids. Most species are relatively fertile, but several have little or no good pollen.

A few of the species hybrids are fertile, but most show a high degree of pollen sterility. Both allo- and autopolyploids are found in the genus.

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