

A TAXONOMIC STUDY OF *SPIRAEA PYRAMIDATA* GREENE (ROSACEAE)

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Spiraea pyramidata was described by Greene (1892) and sixteen years later Rydberg (1908) suggested that it was a hybrid between *S. menziesii* Hook. and *S. lucida* Greene. Other investigators have made the same suggestion based on characteristics which appear to be intermediate between the putative parents such as inflorescence shape, petal color, amount of pubescence, leaf shape, and plant size. This investigation was undertaken to see if tangible evidence might be accumulated to determine the origin and taxonomic status of *S. pyramidata*. The methods used were field study, analysis of morphological data based on mass collections, cytological study of microsporocytes, pollen viability tests, and experiments in hybridization of the suspected parents in the greenhouse.

The suspected parents are geographically sympatric but ecologically allopatric. *Spiraea menziesii*, considered by Presl (1851) to be a variety of *S. douglasii* Hook., and treated similarly here, ranges throughout the Cascades from Alaska to northern California, east to eastern British Columbia and central Idaho. This taxon usually occurs on the flood plains of streams, lake margins, drainage ditches, wet banks, and poorly drained fields. Mainly east of the Cascade crest, *S. lucida* extends from central British Columbia to north central Oregon, and eastward to South Dakota, Wyoming, and Saskatchewan. Normally, it is adapted to open or semi-open, dry and sometimes sandy areas with very little undercover growth. The putative hybrid ranges from central British Columbia southward, mostly east of the Cascade crest, to northeastern Oregon and central Idaho. It is almost always found on disturbed areas such as roadsides, highways, railways, forest camps, and homesites with either suspected parent or both.

MORPHOLOGICAL COMPARISONS. The three taxa are easily distinguished from one another based on reproductive characters. *Spiraea lucida* has a flat, corymbose inflorescence as long as wide, white petals, sepals erect, usually 20 stamens, and 10 staminodia. *Spiraea douglasii* var. *menziesii* has a paniculate inflorescence that is several times longer than wide, red petals, sepals reflexed, usually 30 stamens, and no stam-

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Table 1. STATISTICAL COMPARISONS OF RATIOS OF CHARACTERS IN THREE TAXA OF SPIRAEA

Character		<i>S. douglasii</i> <i>menziesii</i>	<i>S. lucida</i>	<i>S. pyramidata</i> (Washington)	<i>S. pyramidata</i> (Canada)
leaf width/length	mean	38% (33) ²	55% (41)	48% (53)	44% (64)
	st. dev.	±4.1%	±8.0%	±7.3%	±6.4%
	significance ³	+	+	+	+
serration down/ leaf length	mean	32% (33)	53% (41)	52% (55)	31% (58)
	st. dev.	±14.0%	±13.0%	±9.9%	±17.7%
	significance	— to <i>S.</i> <i>pyr.</i> (Can.)	— to <i>S.</i> <i>pyr.</i> (Wash.)	— to <i>S.</i> <i>lucida</i>	— to <i>S. D. var.</i> <i>menziesii</i>
inflorescence width/length	mean	29% (33)	134% (41)	63% (53)	59% (64)
	st. dev.	±7.6%	±23.0%	±22.0%	±21.5%
	significance	+	+	— to <i>S.</i> <i>pyr.</i> (Can.)	— to <i>S.</i> <i>pyr.</i> (Wash.)
petal width/length	mean	72% (33)	80% (42)	76% (50)	74% (58)
	st. dev.	±14.0%	±12.0%	±12.8%	±17.8%
	significance	— to both <i>S. pyr.</i>	— to both <i>S. pyr.</i>	— to all	— to all
style length/ ovary length	mean	132% (32)	182% (40)	154% (50)	141% (48)
	st. dev.	±17.9%	±31.3%	±21.2%	±17.3%
	significance	+	+	+	+

² Numbers within parentheses are the total plants examined.³ + = A significant difference in the character is realized between the taxa 99% of the time.

— = No significant difference in the character is realized between the taxa 99% of the time.

inodia. The putative hybrid has a pyramidal panicle inflorescence less than twice as long as wide, white to pink petals, sepals reflexed, 20-30 stamens, and 10-15 staminodia. Occasionally *S. pyramidata* resembles *S. douglasii* var. *menziesii* in inflorescence shape and flower color, but it always differs in having staminodia.

Vegetatively, the suspected parents are easily distinguishable whereas *S. pyramidata* is less so, particularly from *S. douglasii* var. *menziesii*. *Spiraea lucida* is $\frac{1}{2}$ -2 feet tall, glabrous on the stems and leaves, leaves that are commonly ovate-elliptic and coarsely (singly to doubly) serrate. *Spiraea douglasii* var. *menziesii* is 3-6 feet tall, pubescent on the stems and leaves, the leaves being oblong-elliptic and remotely (singly) serrate. The intermediate taxon is 2-4 feet tall, glabrous to slightly pubescent on the stems and leaves, and with ovate-lanceolate to obovate-elliptic leaves which are finely to coarsely serrate. In order to formulate a more objective basis for conclusions concerning the status of *S. pyramidata*, statistical information was accumulated. Ratios, of leaf width to leaf length, of distance that the serrations extend from the apex of a leaf as compared with total blade length, of inflorescence and petal width versus length, and of style length contrasted with ovary length, permitted one to use the same scale for comparisons. From these data, averages, standard deviations, and significance (Freund 1952) were determined for various populations and groups of populations and are presented in Table 1.

The statistical information is of more interest when plants of *S. pyramidata* from Washington and British Columbia were treated separately. The suspected parents were significantly different from one another in all five characters selected. They were also significantly different from *S. pyramidata* in leaf width over length and style length vs. ovary length but were not significantly different in petal width over length. In the serration character, *S. douglasii* var. *menziesii* was not significantly different from *S. pyramidata* from British Columbia nor was *S. lucida* significantly different from *S. pyramidata* from Washington. The suspected hybrids were significantly different from one another in leaf width over length, serration character, and style-ovary length ratio but not in inflorescence and petal shape. Mean comparisons of the 5 characters tend to show the Canadian populations of *S. pyramidata* to be more closely related to *S. douglasii* var. *menziesii*. These data in addition to field study indicate that introgression toward the latter taxon has occurred in the British Columbia populations.

Data based on Anderson's (1936) hybrid index were accumulated using 10 characters listed in Table 2. Values of 0 were assigned for each character if typical of *S. douglasii* var. *menziesii* and a maximum of 1, 2, 3, or 5 was assigned for a character if typical of *S. lucida*, the total for each plant resulting in a range from 0-21. Such characters as petal color and inflorescence shape were given the highest values because of their

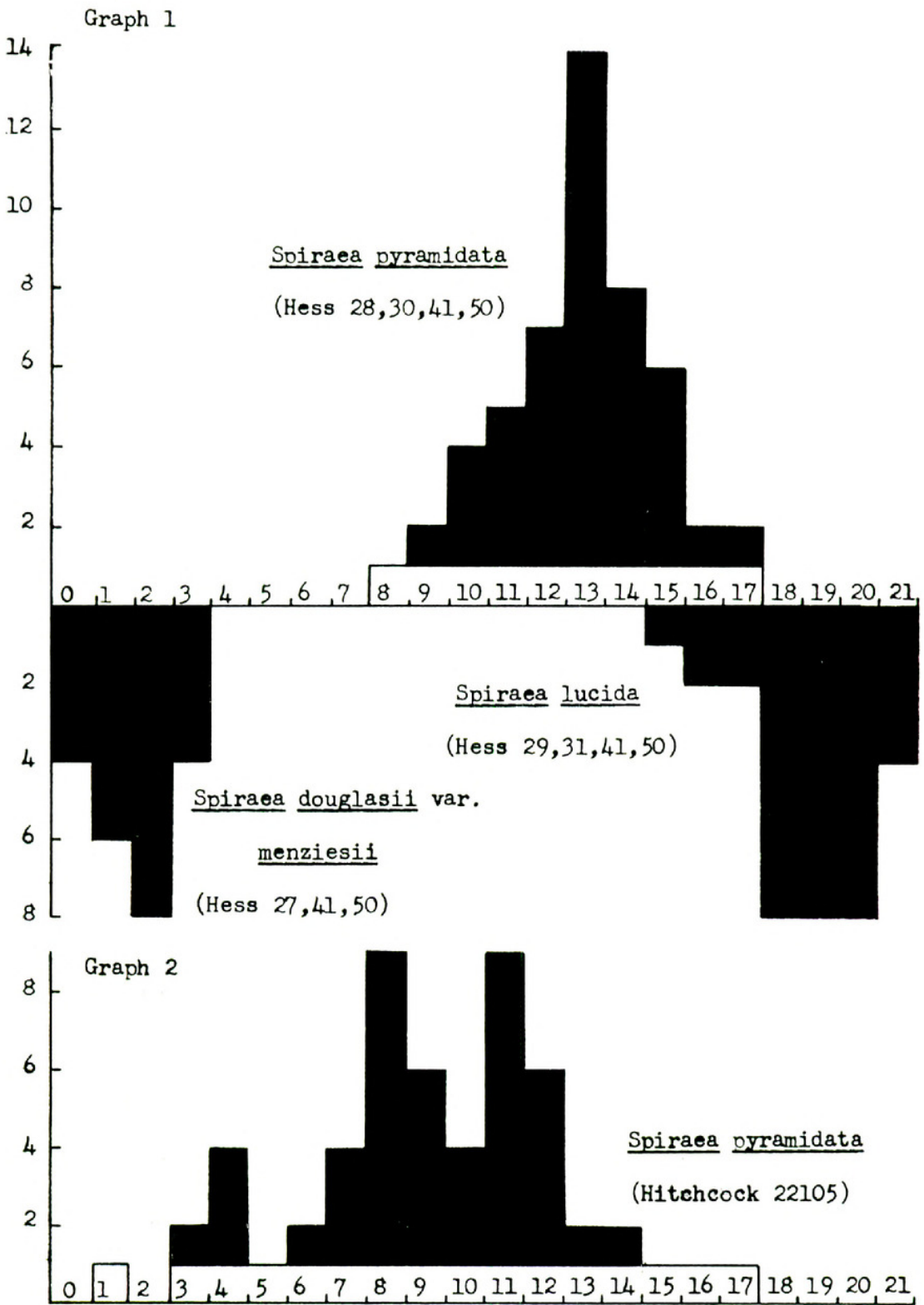
distinct amount of variation. Most others, because of their less distinct variation were given a value from 0-2 and the least distinctive characters a value of 0 or 1.

After the plants had been identified, their ten characters were scored and their index determined. Graph 1 shows the index values for seven collections from 3 different areas in Washington. Found on the upper end of the index scale is *S. lucida* with *S. douglasii* var. *menziesii* on the lower end. Plants identified as *S. pyramidata* are in the center of the scale and slightly skewed toward *S. lucida*. The skewness may be explained by backcrossing and subsequent examination of the introgressants, or the F_1 's in which the progeny resemble the pistillate parent somewhat more than the staminate one, or an error in judgment in assigning values to the characters. *Spiraea lucida* seemed more variable than *S. douglasii* var. *menziesii*, due perhaps to insufficient sampling or to contamination by genes from *S. douglasii* var. *menziesii* via a *S. pyramidata* bridge.

A British Columbian mass collection, composed mostly of *S. pyramidata*, is shown in graph 2. These index values which are throughout the scale may be contrasted with those of *S. lucida* and *S. douglasii* var. *menziesii* in graph 1. Two major peaks in frequency are evident, one somewhat similar to the peak formed by the mass collections of *S. pyramidata* from Washington, the second skewed toward *S. douglasii* var. *menziesii*. The second peak is probably evidence for introgressive hybridization of *S. pyramidata* with *S. douglasii* var. *menziesii*. A complete bridge between *S. lucida* and *S. douglasii* var. *menziesii* via *S. pyramidata* probably allows for genes to flow in the direction of either parent.

POLLINATORS. Visitors to *S. lucida* flowers are mainly beetles (*Mordella atrata* Melsh., *Pentaria trifasciata* Melsh., and *Orphilus niger* Rossi)⁴ and occasionally bees (*Bombus* sp.). Flat topped inflorescences are particularly adapted for the landing of the "poor-flying" beetles according to van der Pijl (1960). The beetles randomly move about from flower to flower in the inflorescence, possibly feeding on the large, fleshy outgrowths just inside the rows of fertile stamens. These structures, believed to be staminodia, probably constitute an adaptive development. The beetles become covered with pollen shed from anthers they have touched, later contacting stigmas of various flowers of *S. lucida* and thereby effecting pollination. The occasional bee visitors spend little time on any one flower, but move from one inflorescence to another. Bees were the only observed visitors to *S. douglasii* var. *menziesii*. There was no discernible pattern to their flower visitation and they moved from flower to flower and inflorescence to inflorescence. Bees are probably responsible for intraspecific and interspecific hybridization

⁴ Beetle identification was made by D. M. Hatch, Zoology Department, University of Washington.



since they are common to both suspected parents. Both bees and beetles visit the flowers of *S. pyramidata*. The staminodia probably account for the presence of the beetles and possibly a part of the same mechanism that attracts bees to *S. douglasii* var. *menziesii* accounts for their

Table 2. INDEX VALUES FOR TEN CHARACTERS

	<i>S. douglasii</i> var. <i>menziesii</i>	<i>S. lucida</i>
leaf shape	0	2
internode length	0	1
singly or doubly serrate	0	1
size of serrations	0	1
inflorescence shape	0	3
inflorescence vesture	0	2
petal shape	0	2
petal color	0	5
presence of staminodia	0	2
style to ovary ratio	0	2
	—	—
	0	21

Table 3. POLLEN FERTILITY

Species	Collection	% Pollen Fertility		No. Plants Examined
		Range	Average	
1. <i>S. douglasii</i> var. <i>menziesii</i>	Hess 17.	80-94	88	11
2. <i>S. lucida</i>	Hess 44.	71-89	84	5
3. <i>S. douglasii</i> var. <i>menziesii</i>	Hitchcock 22059, 22103, 22105, 22113, 22114. Hess 23, 35, 37, 42, 48, 50.			
4. <i>S. lucida</i>	Hitchcock 22059, 22102, 22105, 22114. Beamish et al 1470, 1484. Hess 24, 29, 31, 36, 37, 48, 50.	39-90	64	25
5. <i>S. pyramidata</i>	Hitchcock 22043, 22045, 22060, 22103, 22105, 22111, 22113. Beamish et al 1470, 1488. Hess 9, 22, 28, 30, 34, 37, 48, 50.	0-41	14	45



Fig. 1. Camera lucida drawings of chromosomes from microsporocytes of *Spiraea*. A. *Spiraea lucida*, Kruckeberg 4964. Diakinesis, 18_{II}. B. *Spiraea douglasii* var. *menziesii*, Hess 50. Metaphase I, 18_{II}. C. *Spiraea pyramidata*, Hess 34. Diakinesis, 10_{II}+16_I. D. *Spiraea pyramidata*, Beamish et al 8807. Metaphase I with precociously separated bivalents. E. *Spiraea pyramidata*, Hess 37. Diakinesis, 18_{II}. F. *Spiraea pyramidata*, Hess 34. Late telophase II with micronuclei indicated by the arrows. G. *Spiraea pyramidata*, Hess 49A. Diakinesis, 18_{II}. Greenhouse grown plants from seed collected in the field of *S. pyramidata* (Hess 37). H. *Spiraea densiflora*, Hess 39. Diakinesis, 9_{II}.

presence. Outbreeding as well as inbreeding (both geitonogamous and autogamous) among the three taxa occurs due to the two pollinators.

POLLEN STAINABILITY. Stamens were removed from dried flowers and squashed in cotton blue-lactophenol and the number of pollen grains that stained well were counted. The staining is interpreted as evidence for fertile pollen grains.

Pollen fertility of the various taxa is listed in Table 3. The first two collections, which represented pure and well isolated populations, showed a high pollen fertility. Each of the next 3 groupings of collection numbers represented mixed mass collections. The fertility range of *S. douglasii* var. *menziesii* and *S. lucida* in these mixed populations was considerably greater than in the pure populations. The fertility of *S. pyramidata* was also variable. An explanation of the wide stainability range may be that backcrossing of the putative hybrid with the suspected parents has produced plants (introgressants) similar in morphology to the three taxa but cytologically variable.

CYTOLOGY. The cytological information was obtained from bud material collected in the field, from greenhouse grown plants at the University of Washington, and from material sent from the University of British Columbia through the kindness of Dr. K. Beamish. Those buds personally collected were fixed in vials containing freshly prepared 3 parts 95% ethanol and 1 part glacial acetic acid, and stored in a refrigerator no later than 10 days after collection.

Counts were made of each taxon from at least four different areas. Buds that showed the best meiotic figures were from 1-2 mm. in length. Temporary mounts were made of anthers squashed in aceto-carmine stain. Microsporocytes that showed the desired meiotic figures were drawn with the aid of a camera lucida apparatus. After cytological examination the temporary mounts were made permanent by the alcohol exchange-euperal method of Bradley (1948).

The basic chromosome number for *Spiraea* is 9 (Darlington and Wylie, 1955). Four counts of New World species by Sax (1936) indicate three of them tetraploids and the other a triploid. Bowdin (1945) reported another New World species to be a tetraploid. Table 4 lists the chromosome numbers of the three pertinent taxa involved in this investigation plus *S. densiflora* Nutt. ex T. and G. because of its general interest. Figure 1 shows camera lucida drawings of the four taxa. Eighteen bivalents were consistently noted in the microsporocytes of *S. lucida* and *S. douglasii* var. *menziesii*. The somatic chromosome number of *S. pyramidata* totaled 36, consisting of either 18 bivalents or mostly of combinations of bivalents and univalents. The anthers of some flowers had microsporocytes with both 18 bivalents and combinations of bivalents and univalents. The presence of precocious separations and micronuclei in the pollen tetrads was also evidenced (Fig. 1). This would account for low pollen fertility in the hybrid.

Table 4. SOMATIC CHROMOSOME NUMBER

<i>Species</i>	$2n$	<i>Source of Preserved Material</i>
<i>S. douglasii</i> var. <i>menziesii</i>	36	Washington: Chelan Co., Hess 10, 11, 12, 42; Whatcom Co., Hess 50. British Columbia: Yale District, Hitchcock 22061; Wells District, Beamish et al 8809.
<i>S. lucida</i>	36	Washington: Okanogan Co., Hess 44; Whatcom Co., Hess 50; Kittitas Co., Kruckeberg 4964. British Columbia: Wells District, Beamish et al 8808.
<i>S. pyramidata</i>	36	Washington: Kittitas Co., Hess 37; Plants grown from seed of Hess 37, 49. British Columbia: Yale District, Hitchcock 22060, 22045; Wells District, Beamish et al 8807, 8810.
<i>S. pyramidata</i>	36 $9_{II}+18_I$	Washington: Chelan Co., Hess 9, 30.
<i>S. pyramidata</i>	36 $10_{II}+16_I$	Washington: Yakima Co., Hess 34. British Columbia: Wells District, Beamish et al 8810.
<i>S. pyramidata</i>	36 $11_{II}+14_I$	British Columbia: Wells District, Beamish et al 8799.
<i>S. pyramidata</i>	36 $13_{II}+10_I$	Washington: Chelan Co., Hess 28.
<i>S. pyramidata</i>	36 $14_{II}+8_I$	British Columbia: Wells District, Beamish et al 8807.
<i>S. densiflora</i>	18	Washington: Pierce Co., Hess 39.

It was of interest to note that *S. densiflora* was a diploid with 18 chromosomes. This is the first report of a diploid *Spiraea* in the New World, although Sax (op. cit.) reports 11 diploids of the genus in the Old World. The suspected hybrid between *S. douglasii* var. *menziesii* and *S. densiflora* is of particular interest for further study. It is possibly a triploid yet is similar morphologically to some suspected introgressants of *S. pyramidata* which are tetraploids. Future investigations will include this aspect of research.

GREENHOUSE STUDY. In the summers of 1960 and 1961 seeds, cuttings, and live plants of the three taxa were collected in the field. Attempts were made to grow them in the greenhouse, the ultimate object being to duplicate the natural hybrid by artificial means, if possible. The suspected hybrid and *S. douglasii* var. *menziesii* grew well from

cuttings, field transplants, and seeds. Field transplants and progeny from the seeds of *S. lucida* grew well but only 3 of 70 cuttings survived. Plants that developed from seed reached flowering stage after 6-8 months of development.

The seeds from *S. pyramidata*, which were collected in the field, developed into plants that resembled *S. lucida* in size and inflorescence shape. Some had normal appearing flowers but a few had leafy calyx lobes and petals, few stamens, and only 2 or 3 carpels. The latter condition is not considered to be uncommon in greenhouse grown plants.

In the summer of 1961 artificial reciprocal crossings involving *S. lucida*; the plants grown therefrom in the greenhouse appeared to be tendency of greenhouse grown plants of the latter species to wilt only one set of crosses was made. Emasculation performed on the flowers just before anthesis was difficult since the flowers were small and stamens numerous. Hand pollination was effected periodically over three days. The carpels of *S. douglasii* var. *menziesii* apparently do not mature until spring and early summer so no seeds at the time of the study had been acquired. On the other hand, seeds had been produced on *S. lucida*; the plants grown therefrom in the greenhouse appeared to be vegetatively intermediate to the parents or similar to *S. pyramidata*. Observations of the developing inflorescence corroborated the intermediate nature of the hybrid; however, the author had to leave before full development was realized. Further verification was not obtained.

SUMMARY. The hybrid-origin hypothesis has been substantiated by evidence derived from field study of the pollinators and the hybrid environments, cytological investigations that have disclosed univalent and bivalent chromosomes, precocious separations of chromosomes in pollen mother cells, and micronuclei in spore tetrads, tests of pollen viability, morphological examinations, statistical studies such as hybrid indices, and controlled artificial hybridization.

Spiraea douglasii var. *menziesii* and *S. lucida* were successfully crossed in the greenhouse. The viable seeds produced grew into two dissimilar sets of plants, one of which consisted of seedlings that apparently would not survive in natural surroundings, the other of larger and more vigorous plants that would have a much greater chance for survival in natural conditions. The vegetative characteristics of the more robust plants were similar to those of *S. pyramidata*. There is no reason to doubt that hybridization is occurring constantly between the suspected parents and only if the seed falls in a disturbed habitat will there be any selective advantage. Once the hybrid is established, it spreads extensively by rhizomes but only in the open and disturbed areas.

There is little indication for introgression in Washington, since *S. pyramidata* was collected in 1892 around "Clealum", and currently it seems to show no introgression in that area. It probably became estab-

lished during some habitat disturbance where it persisted and spread vegetatively. In contrast, introgression seems not uncommon in British Columbia. No explanation is available as to why introgression was evident in British Columbia and not in Washington. On route 90, 7 miles north of Quesnel, British Columbia, a large mixed population of *S. pyramidata*, *S. douglasii* var. *menziesii*, occasional *S. lucida*, and apparently introgressants extends for several miles. After the hybrid had been established, possibly a second disturbance created another "hybridized habitat" and seedlings of introgressants were then able to become established. As long as the introgressants are recognizable as the hybrid, it seems reasonable to include them as part of *S. pyramidata*.

Spiraea pyramidata, a tetraploid, is the result of an interspecific cross between two tetraploids and is strikingly different morphologically, physiologically, genetically, and ecologically from either parent. Although widespread, it occurs only in areas where the parents have come together in a disturbed habitat. There is little morphological variation between individuals of the same population and only slightly more variation between different populations. The plants are perennials that spread by a strong rhizome system. The phenotypic pattern is apparently similar from population to population and because of some sterility factors few intergradient populations are formed through back-crossing. It is proposed that the taxon be accorded status as *S. × pyramidata* (*S. douglasii* × *S. lucida*) Greene, a term that portrays its origin.

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