LILAC SPECIES HYBRIDS

KARL SAX

With one plate

THERE is a remarkable correlation between the taxonomic classification of the species of *Syringa* and the genetic affinities of the species. In Mrs. McKelvey's monograph (1928) of the lilacs, the genus was separated by Rehder into two sections, two series, and two subseries. No hybrids have ever been obtained from crosses between species of different sections, series, or subseries, but within these units there is considerable genetic compatability.

More recently, Redher (1945) has indicated that the sections are worthy of subgeneric rank, as *Eusyringa* and *Ligustrina*. The subgenus *Eusyringa* is divided into four series, the *Villosae, Pubescentes, Vulgares,* and *Pinnatifoliae*. The *Pinnatifoliae* have been separated from the *Vulgares* on morphological grounds, although there is considerable genetic compatability between these two series. The *laciniata* variety of *S. persica* has been raised to specific rank, and the typical *S. persica* and its entire-leaved varieties are now classed as hybrids. The nomenclature used in this survey is based upon Rehder's classification of the genus (McKelvey, 1928; Rehder, 1945).

Crosses have been made between various species of *Syringa,* but most of them have been made between rather closely related species. Improved types of lilacs of the *Villosae* series have been obtained from crosses between *S. Josikaea* and *S. villosa* made by L. Henry, and from crosses between *S. reflexa* and *S. villosa* which have produced the various forms of the *S. Prestoniae* hybrids. Within the *Vulgares* series crosses between *S. oblata* and *S. vulgaris* have given rise to the hybrid *S. hyacinthiflora* and to the various Lemoine hybrids, but these hybrids differ from the common lilacs only in the time of flowering and a few other minor characters. The only new distinctive types of lilacs of ornamental value have been obtained from crosses between *S. laciniata* and *S. vulgaris*.

Within the subgenus *Eusyringa* there is more or less genetic compatability between species. In the *Villosae* series there are nine species. All are of Asiatic origin with the exception of *S. Josikaea,* which is a native of the Carpathian Mountains. Five of the nine species, including *S. Josikaea,* have been used in various combinations to obtain species hybrids, and it is possible that all of the *Villosae* species are inter-fertile to some degree. However, even the species crosses which produce some vigorous hybrids also produce some abnormal plants. According to Miss Preston (McKelvey, 1928), the cross between *S. reflexa* and *S. villosa* results in a large proportion of dwarf and variegated progeny as well as plants which are very vigorous.

The species of the *Pubescentes* series are all of Asiatic origin and many of them are rather similar in general morphological characters; yet species hybridization in this group of lilacs is limited. During the past fifteen years we have attempted to combine the fragrance of *S. pubescens* with the more attractive flowers of *S. velutina, S. Potanini, S. microphylla,* and other species. Many of the crosses produce viable seeds, but the seedlings are albinos and soon die. Occasionally a variegated seedling survives but grows slowly. Several hybrid plants from the cross of *S. velutina* × *S. pubescens* have survived for ten years, but they are small and poorly developed. A cross between *S. pubescens* and *S. Potanini* produced a number of seedlings which are now two years old, but they lack vigor and probably will not survive. The only vigorous hybrid obtained in this subseries was from a cross between *S. Potanini* and *S. microphylla,* but this cross also produced some dwarf seedlings. It is possible that certain other combinations would also produce some vigorous hybrids, but as a group there is considerable incompatibility among the species of the *Pubescentes.*

The species of the *Vulgares* series include *S. vulgaris, S. oblata,* and *S. laciniata. Syringa vulgaris* is a native of southeastern Europe, while the other species are indigenous in China. There is considerable genetic affinity among these species. Crosses between *S. vulgaris* and *S. oblata* have produced many vigorous hybrids in the past and we have grown a number of second generation segregates. Both spontaneous and artificial hybrids of *S. vulgaris* and *S. laciniata* have been grown. According to Rehder (1945), a hybrid between *S. oblata* and *S. laciniata* has been found in a garden in Chengchow, China. We have obtained viable seeds from a cross between *S. laciniata* and a variety of *S. oblata.*

The series *Pinnatifoliae* is represented by a single species, *S. pinnatifolia.* Although this is a distinct species, it is rather closely allied to species of the *Vulgares* series. It produces hybrids with *S. oblata* varieties which are vigorous but sterile (Rehder, 1935). It is probable that it will also cross with *S. vulgaris.* We have obtained hybrids between *S. laciniata* and *S. pinnatifolia;* these hybrids are uniform and vigorous.

The hybrids of greatest horticultural value have been obtained from crosses between *S. laciniata* and *S. vulgaris.* The first hybrids were obtained from a spontaneous cross in the Botanical Garden at Rouen. In 1777 Varin, the director of the garden, planted open pollinated seeds of *S. laciniata* and obtained the hybrid first known as the Varin lilac or *S. rothomagensis,* and now known as *S. chinensis.* Varin did not recognize the progeny of the cut-leaved lilac as a natural hybrid of *S. laciniata* × *S. vulgaris,* but considered it as the normal progeny of a degenerate or abnormal form of the Persian lilac (McKelvey, 1928).

At the end of the 19th century, hybrids between *S. laciniata* and *S. vulgaris* were produced through artificial pollination by L. Henry and by E. Lemoine. The hybrids were similar to those obtained by Varin, but varied according to the variety of the *S. vulgaris* parent used in the cross. Mrs. McKelvey recognizes about a dozen forms of *S. chinensis.* Several varie-

ties have originated as bud sports. These hybrids are generally considered to be the most attractive of all lilacs. They tend to resemble the Persian lilac in habit of growth and inflorescence, but the leaves usually are entire, as in the *S. vulgaris* parent. The Chinese lilacs are sterile and there is no conclusive evidence that they have ever produced viable seeds either spontaneously or as the result of artificial pollination.

The subgenus *Ligustrina* of *Syringa* includes three species, all of Asiatic origin. Little is known of their genetic relationships, as they are not of great horticultural interest. We have tried to obtain hybrids between these tree lilacs and species of the *Villosae* and *Vulgares* groups, but with no success.

In view of the remarkable correlation between the taxonomic classification and the genetic compatibility of the species of *Syringa,* the former taxonomic status of the Persian lilac was an enigma. The typical form of *S. persica* is a plant with predominantly entire leaves and resembles × *S. chinensis,* a known hybrid between *S. laciniata* and *S. vulgaris.* It is highly or completely sterile, although L. Henry in 1897 tells of crossing *S. vulgaris* with an entire-leaved Persian lilac and obtaining several dozen seedlings. There is, however, no record of seed production on any of the entire-leaved forms of *S. persica.* The typical form is not a native of Persia, nor has it been found wild in any part of the world. Mrs. McKelvey has shown that it was first recorded in 1660, fifty years after *S. laciniata* was described by a French naturalist, who obtained the variety from Italy as *Ligustrum nigrum.*

In 1900 E. Lemoine suggested that *S. persica* was a hybrid between *S. persica laciniata* and *S. vulgaris.* There is, however, no record of *S. vulgaris* in Persia, either as an indigenous or as an introduced plant, at the time of the origin of *S. persica.* It is possible that the obscure species *S. afghanica* was the entire-leaved parent. There is no doubt that *S. laciniata* was the other parent, because it was the only available species which could have contributed the genes for the occasional cut and laciniate leaves of *S. persica.* Cytological studies by Tischler (1930) and by the author (Sax, 1930) have shown that the meiotic divisions in *S. persica* are very irregular. The evidence from distribution, genetic behavior, and cytological analysis confirms Lemoine's conclusion that the typical *S. persica* is a hybrid and is allied to × *S. chinensis.*

Syringa laciniata is the only Persian lilac known to exist as an indigenous species. It was collected by F. N. Meyer in 1915 in Kansu, China. Seeds sent to the Arnold Arboretum produced plants which, according to Mrs. McKelvey (1928), were identical with the cut-leaved variety long known in cultivation as *S. persica laciniata.* It is evident that the cut-leaved variety is the only true species of Persian lilac and that it is a native not of Persia, but of China. Presumably it was introduced into Persia over the old trade routes from China long before the 17th century.

The entire-leaved Persian lilacs and all varieties of *S. chinensis* grown in the Arnold Arboretum are sterile. Occasionally *S. chinensis* sets a few

partially developed seeds, but none have been viable. We have had no success in crossing these species with either *S. vulgaris* or *S. laciniata*. Earlier cytological studies (Sax, 1930) showed great cytological irregularity at meiosis with about 12 bivalents and 12 univalents. Since all pure species of *Syringa* have 22–24 pairs of chromosomes, the apparent cytological behavior of the hybrids was difficult to explain. More recent studies show that the normal chromosome number is present at diakinesis, but the pairing is loose and irregular.

Our crosses between *S. laciniata* and *S. vulgaris* have set seeds and most of the seedlings have lived for one or two years, but we have obtained no mature plants. In 1939 and in 1940 open pollinated seeds were collected from the only remaining specimen of *S. laciniata* in our collections. A total of 243 plants was grown. Of these only six had the cut leaves characteristic of the seed parent. These seedlings during the first few years were entirely cut-leaved and the leaves were more pinnate than those of the mature seed parent. In fact, these plants appeared to be a new and distinct type of lilac. In the fifth year, however, these segregates lost their juvenile characters and began to resemble the mature maternal parent, and were very similar to four-year-old cuttings from the parent plant. The transition from the juvenile form to the mature plant is shown in *Figure 1*. These seedlings are fertile and are undoubtedly the result of self-pollination which reproduces the parental species.

The remaining 237 seedlings all were predominantly entire-leaved as they developed. Most of these plants survived for only one or two years and only five have survived to 1944. Two of the survivors have flowered but have set no seeds. In every respect they resemble *S. chinensis* and certain forms of *S. persica* except that they are less vigorous. The leaf types of the two parents and of a form of *S. chinensis* are shown in *Figure 2*. The entire-leaved seedlings must be spontaneous hybrids between *S. laciniata* and the surrounding specimens of *S. vulgaris*. The fact that most of the seedlings were weak and did not survive apparently is not unusual in this and other species hybrids of *Syringa*. Although Varin is reported to have planted open pollinated seeds of *S. persica laciniata* for many years and no doubt Lemoine made many artificial crosses, yet we have only about a dozen varieties of the hybrids. Since there are hundreds of varieties of *S. vulgaris*, an equal number of *S. chinensis* hybrids could be obtained if the cross were fully compatible. Apparently *S. laciniata* is highly, but not completely, self-sterile. It sets a few selfed seeds, but is usually cross-pollinated, and will cross spontaneously with adjacent specimens of *S. vulgaris*. Most of the resulting seeds are viable, but only a few develop into vigorous mature plants.

Syringa chinensis and *S. persica* have predominantly entire leaves, but all forms have some lobed or laciniate leaves. The prevalence of entire leaves varies in different varieties of the hybrids. The frequence of cut leaves appears to depend upon the vigor of the plant, and different branches of the same plant may vary greatly in leaf form. The leaf types

of mature hybrids are shown in *Figure 3*. These specimens are from different plants, but similar variation often can be found on the same plant.

Further evidence of the genetic nature of *S. laciniata* is provided by the results of crossing with *S. pinnatifolia*. The F_1 seedlings are vigorous and uniform. The leaves of the parents and the hybrid are shown in *Figure 4*. The twigs of the parent species are from mature plants, while that of the F_1 is from a two-year-old seedling. As the hybrid matures the leaf characters may become more intermediate. The uniformity of the eight F_1 plants indicates that both parents are relatively homozygous. *Syringa pinnatifolia* is highly self-sterile and sets seed only when pollinated by adjacent *S. oblata* (Rehder, 1935) or perhaps *S. vulgaris* plants. The natural hybrids are relatively uniform and are sterile, but are of little horticultural value. The *S. laciniata* × *S. pinnatifolia* hybrids are attractive shrubs and should be of considerable horticultural value if the flowers prove to be at all attractive.

SUMMARY

There is a remarkable correlation between the taxonomic classification of the genus *Syringa* and the genetic compatibility of the 28 species. With one exception the species which belong to different subgenera and series have not been crossed spontaneously or by artificial pollination. Species within these taxonomic units show considerable genetic compatibility, although many of the hybrids often lack vigor and most of them are sterile. *Syringa pinnatifolia,* the sole species of the *Pinnatifoliae* series, can be crossed with *S. oblata* and *S. laciniata* of the *Vulgares* series, but is placed in a distinct series on morphological grounds.

The species hybrids of greatest horticultural value have been obtained from crosses between *S. laciniata* and *S. vulgaris* and are known as × *S. chinensis*. The entire-leaved Persian lilacs also are hybrids involving *S. laciniata* and an entire-leaved species — *S. afghanica* or *S. vulgaris*.

LITERATURE CITED

Anderson, E. and A. Rehder. New hybrids from the Arnold Arboretum. Jour. Arnold Arb. 16: 358–363. 1935.

McKelvey, S. D. The Lilac. 581 pp., *172 pl.* The MacMillan Co., New York. 1928.

Rehder, A. Notes on some cultivated trees and shrubs. Jour. Arnold Arb. 26: 67–78. 1945.

Sax, Karl. Chromosome number and behavior in the genus Syringa. Jour. Arnold Arb. 11: 7–14. *1 pl.* 1930.

Tischler, G. Ueber die Bastardnatur des persichen Flieders. Zeit. für Bot. 23: 150–162. *10 fig.* 1930.

EXPLANATION OF PLATE I

FIG. 1. Variation in foliage of *S. laciniata*. Juvenile stage at left from a four-year-old seedling. Transitional stage in center from five-year-old seedling. At the right are three specimens from the same mature plant. FIG. 2. Foliage of *S. laciniata* and *S. vulgaris*, with the hybrid *S. chinensis* between. FIG. 3. Variation in foliage of *S. persica*. These specimens were from different varieties, but similar variation often can be found on a single plant. FIG. 4. Foliage of *S. laciniata* (left) and *S. pinnatifolia* (right), and of the F_1 hybrid seedling.

ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

Lilac Species Hybrids