J. Amer. Soc. Hort. Sci. 142(4):279–288. 2017. doi: 10.21273/JASHS04155-17

Intraspecific, Interspecific, and Interseries Cross-compatibility in Lilac

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Additional index words. *Syringa*, *Pubescentes*, *Villosae*, in vitro germination, controlled crosses, wide hybridization

Abstract. **Lilacs (*Syringa* sp.) are a group of ornamental trees and shrubs in the Oleaceae composed of 22–30 species from two centers of diversity: the highlands of East Asia and the Balkan-Carpathian region of Europe. There are six series within the genus *Syringa*: *Pubescentes*, *Villosae*, *Ligustrae*, *Ligustrina*, *Pinnatifoliae*, and *Syringa*. Intraspecific and interspecific hybridization are proven methods for cultivar development. However, reports of interseries hybridization are rare and limited to crosses among taxa in series *Syringa* and *Pinnatifoliae*. Although hundreds of lilac cultivars have been introduced, fertility and cross-compatibility have yet to be formally investigated. Over 3 years, a cross-compatibility study was performed using cultivars and species of shrub-form lilacs in series *Syringa*, *Pubescentes*, and *Villosae*. A total of 114 combinations were performed at an average of 243 ± 27 flowers pollinated per combination. For each combination, we recorded the number of inflorescences and flowers pollinated as well as number of capsules, seed, seedlings germinated, and albino seedlings. Fruit and seed were produced from interseries crosses, but no seedlings were recovered. A total of 2177 viable seedlings were recovered from interspecific and intraspecific combinations in series *Syringa*, *Pubescentes*, and *Villosae*. Albino progeny were produced only from crosses with *Syringa pubescens* ssp. *patula* 'Miss Kim'. In vitro germination was attempted on 161 seed from interseries crosses, resulting in three germinations from *S. pubescens* Bloomerang® x *Syringa vulgaris* 'Ludwig Spaeth'. None survived, yet cotyledons produced callus for future efforts to induce embryogenic shoots. This study is a comprehensive investigation of lilac hybridization, and the knowledge gained will aid future efforts in lilac cultivar development.**

Syringa is a diverse genus in the olive family (Oleaceae) representing 22–30 species from two centers of diversity: the highlands of East Asia and the Balkan-Carpathian region of Europe (Kochieva et al., 2004). Most lilacs are native to Asia, whereas *S. vulgaris* and *S. josikaea* are native to southeastern Europe (Kim and Jansen, 1998). Hundreds of cultivars have been produced and are ubiquitous in temperate gardens around the world. Historically, the most popular cultivars originated *S. vulgaris,* primarily grown for its fleeting spring blooms of purple, pink, blue, or white fragrant flowers. Previous phylogenies have divided lilacs into subgenera and four series (Rehder, 1945) which were later confirmed as monophyletic groups using plastid DNA (Kim and Jansen, 1998). The current phylogeny by Li et al. (2012) based on nuclear and plastid DNA sequences recognizes six series: *Pubescentes*, *Villosae*, *Ligustrina*, *Ligustrae*, *Pinnatifoliae*, and *Syringa* (*Vulagares*).

Each series has distinguishing morphological features. Series *Syringa* is unique by having simple, glabrous leaves while series *Pubescentes* has pubescent leaves (Li et al., 2012). Series *Villosae* is distinct by having inflorescences develop from a single terminal bud with lateral, vegetative buds (Kim and Jansen, 1998). *Ligustrina* differs by its privet-like flowers (short, white corolla tubes with exerted anthers) and growth habit as a tree (Kim and Jansen, 1998). *Pinnatifoliae* is distinguished by having pinnately compound leaves (Li et al., 2012). *Ligustrae* contains several privets (*Ligustrum* sp.) nested within the lilacs (Li et al., 2012).

Lilacs are of major economic importance to the United States nursery industry. In 2014, nationwide sales topped 1.8 million generating more than $20 million in total revenues (U.S. Department of Agriculture, 2016). Intraspecific and interspecific hybridization have proven to be valuable methods for the development of lilac cultivars. Interspecific hybridization has been particularly useful at producing cultivars with improved flowering and new foliar phenotypes (Table 1). Lilac breeding was scarce before the 1800s, a time when selections focused on improved form, flower color, or spring flush in chance seedlings (Fiala and Vrugtman, 2008). Early advancements in breeding produced vigorous interspecific hybrids including *S. ×hyacinthiflora* from crosses between *S. oblata* and *S. vulgaris* by the Lemoine nursery (Lemoine, 1878; Sax, 1930). This nursery was responsible for 214 cultivars and caused a spike in popularity of lilacs in the 1900s (Fiala and Vrugtman, 2008). Many breeders emerged to produce cultivars with a wide range of ornamental traits. Descanso Gardens in southern California and the United States National Arboretum focused on improving *S. ×hyacinthiflora* hybrids for southern climates by incorporating low chilling requirements and powdery mildew resistance (Fiala and Vrugtman, 2008).

Cultivar improvement in series *Villosae* began its ascendancy with complex interspecific hybridization involving *S. reflexa* by Isabella Preston in Ottawa, ON, Canada (Fiala and Vrugtman, 2008). A total of 47 cultivars were introduced

Received for publication 3 May 2017. Accepted for publication 5 June 2017.
This research was funded in part by the Oregon Department of Agriculture Nursery Research Grant Program.
We wish to thank Mara Friddle, Kim Shearer, Aleen Haddad, and the entire staff of the Ornamental Plant Breeding Lab at Oregon State University for technical support.
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Table 1. Interspecific hybrids in lilac and their parent species (Fiala and Vrugtman, 2008).

Interspecific hybrid	Parent 1	Series	Parent 2	Series
Syringa ×chinensis	*S. protolaciniata*	*Syringa*	*S. vulgaris*	*Syringa*
Syringa ×diversifolia[z]	*S. pinnatifolia*	*Pinnatifoliae*	*S. oblata* ssp. *oblata*	*Syringa*
Syringa ×henryi	*S. josikaea*	*Villosae*	*S. villosa*	*Villosae*
Syringa ×hyacinthiflora	*S. oblata*	*Syringa*	*S. vulgaris*	*Syringa*
Syringa ×josiflexa	*S. josikaea*	*Villosae*	*S. reflexa*	*Villosae*
Syringa ×laciniata	Unknown	Unknown	Unknown	Unknown
Syringa ×nanceiana	*Syringa ×henryi*	*Villosae*	*Syringa sweginzowii*	*Villosae*
Syringa ×persica	Unknown	Unknown	Unknown	Unknown
Syringa ×prestoniae	*S. villosa*	*Villosae*	*S. komarowii*	*Villosae*
Syringa ×swegiflexa	*S. komarowii*	*Villosae*	*S. sweginzowii*	*Villosae*

[z]Interseries hybrid.

from the interspecific hybrids *S. ×prestoniae* and *S. ×josiflexa*, which were created by crossing several species in series *Villosae* (*S. villosa*, *S. reflexa*, and *S. josikaea*) (Table 1) (Fiala and Vrugtman, 2008). One of Preston's contemporaries, Frank Skinner, produced similar interspecific hybrids in *Villosae*, several of which are still available in the trade (Fiala and Vrugtman, 2008).

Ornamental traits in series *Pubescentes* have been noted since the early 1900s when director of the Arnold Arboretum, Charles Sargent, noted in a wild-collected specimen of *S. pubescens*, "…if it keeps up its habit of flowering a second time in autumn, it will at least be interesting even if other lilacs are more beautiful." Remontancy (or reblooming) as noted by Sargent would become one of the most pursued traits by modern lilac breeders (Fiala and Vrugtman, 2008). Early introductions in series *Pubescentes* exhibited improved form and flowers in addition to cold hardiness from wild-collected *S. pubescens* ssp. *patula* from E.H. Wilson's Diamond Mountain expedition in Korea (Fiala and Vrugtman, 2008). Most new cultivars in series *Pubescentes* are prolific flowering, compact, and disease resistant with several cultivars exhibiting summer remontancy.

In contrast to the success of interspecific hybridization, interseries hybridization has proven more difficult with the only successful hybrids from crosses between taxa in series *Syringa* and series *Pinnatifoliae* (Pringle, 1981). Interseries hybridization has been a goal of breeders for nearly a century, as illustrated by early reports: "…combinations of the early blooming *Syringa vulgaris* varieties with the late *Villosae* species would undoubtedly be of value if they could be made…" (Sax, 1930). Previous attempts to create interseries hybrids resulted in abortive fruit with no germination of recovered seed (Pringle, 1981).

Abortive seed in lilacs has been explored in previous research. Anatomical studies on *S. villosa*, a species with high rates of seed abortion, found that after cross-pollination, embryos developed normally through the globular, heart, torpedo, and cotyledon stages before embryo and endosperm degradation (Chen et al., 2012). Few embryo rescue studies have been attempted in lilacs. However, Zhou et al. (2003) successfully cultured immature embryos on Monnier's medium (Monnier, 1990) supplemented with 1-naphthaleneacetic acid, 6-benzylaminopurine (BAP), glutamine, and a high concentration of sucrose, indicating that tissue culture may be a platform for recovering hybrid lilacs. Even if in vitro germination fails, callus developed from the hybrid tissue may provide another source for producing interseries hybrids. Lilac somatic embryogenesis protocols using cotyledons have recently been developed for *S. reticulata* var. *mandshurica* (Liu et al., 2013).

Although hundreds of improved lilac cultivars have been introduced, fertility and cross-compatibility among cultivars, species, and series have yet to be investigated in a formal study. The objectives of this study were to 1) investigate cross-compatibility of elite cultivars in intraspecific, interspecific, and interseries combinations and 2) investigate the potential for interseries hybridization and in vitro embryo rescue of abortive embryos.

Materials and Methods

Parent material. Parents were collected from nurseries, gardens, and arboreta from 2009 to 2014 (Table 2) that provided cultivar and trademark names. Full scientific names, cultivars, and trademarks are reported (Table 2), but for simplicity only market names (cultivar or trademark) are used hereafter. Taxonomic designations reflect current phylogenies and revisions, including the use of subspecies designations in *Pubescentes* (Chen et al., 2009). Representative species and cultivars were obtained from series *Syringa*, *Pubescentes*, and *Villosae* focusing on elite cultivars improved for ornamental traits including flower colors and forms, leaf pigments, and novel growth habits including dwarf habits.

Flower colors included white, pink, blue, and purple, with one taxon, *S. vulgaris* 'Sensation', having picotee flowers in which the petal edges lack pigment. Flower forms included single and double flowers, with some exhibiting hose-in-hose flowers. Double flowers in lilac often represent a case of neoheterotrophy where additional floral whorls lead to supernumerary petals (Dadpour et al., 2011). Double flowers can also arise from mutations leading to petaloid sepals (Fiala, 1988). Both cases leave reproductive whorls intact and allow for double-flowered cultivars to be used in reciprocal crosses. Foliar pigments were rare across the breeding population, occurring in a spring flush of yellow or purple leaves (Fig. 1). *Syringa emodii* in series *Villosae* was the only taxon that produced a yellow flush of leaves (Fig. 1A). Purple color of spring foliage was limited to purple-flowered taxa in series *Syringa*, but was most pronounced in *S. ×hyacinthiflora* 'Old Glory' (Fig. 1B). Novel variations in form were limited to two dwarf taxa in series *Syringa*, *S. vulgaris* 'Tiny Dancer' and *S. vulgaris* 'Prairie Petite'.

Crosses. During the spring and summer of 2013, 2014, and 2015, a total of 27,645 cross-pollinations were made. Of these, 114 crosses were performed with an average of 243 ± 27 flowers pollinated per cross. For each series, three types of crosses were attempted: intraspecific, interspecific, and interseries (Tables 3–5, respectively). Within each series, crosses made with at least one interspecific parent (e.g., *S. ×hyacinthiflora* x *S. oblata*) were classified as interspecific. Most cultivars in *Villosae* were interspecific hybrids; each replicate of an unimproved species was collected from a single source. For example, we received *S. emodii* from a single Index Seminum source. Consequently, crosses with *Villosae* focused on interseries and interspecific combinations because intraspecific crosses would likely involve significant inbreeding.

Table 2. Source material for lilac breeding population.

Series[z]	Taxon[y]	Cultivar (trademark)	Accession no.[x]	Source[w]
Syringa	*S. oblata*		09-0058	Arborétum Mlyňany
	S. oblata var. *alba*		09-0059	Arborétum Mlyňany
	S. vulgaris	Agincourt Beauty	13-0036	Briggs Nursery
		Agincourt Beauty	14-0124	Dennis' 7 Dees
		Angel White	10-0043	Blue Heron Farm
		Angel White	13-0075	Monrovia
		Monore (Blue Skies®)	13-0076	Monrovia
		Lavender Lady	13-0078	Monrovia
		Ludwig Spaeth	10-0042	Blue Heron Farm
		Ludwig Spaeth	13-0079	Monrovia
		Prairie Petite	13-0035	Briggs Nursery
		President Grévy	10-0040	Blue Heron Farm
		President Grévy	14-0125	Portland Nursery
		President Lincoln	13-0080	Monrovia
		Sensation	13-0081	Monrovia
		Elsdancer (Tiny Dancer)	13-0001	Heritage Seedlings
	S. ×hyacinthiflora	Betsy Ross	13-0034	Briggs Nursery
		Maiden's Blush	14-0123	Dennis' 7 Dees
		Old Glory	13-0085	Monrovia
		Pocahontas	13-0084	Monrovia
Pubescentes	*S. meyeri*	Palabin	10-0209	Bailey Nurseries
	S. pubescens	Penda (Bloomerang® Purple)	12-0026	Garland Nursery
		Penda (Bloomerang® Purple)	13-0070	Monrovia
		Penda (Bloomerang® Purple)	14-0189	Select Plus
		SMSJBP7 (Bloomerang® Dark Purple)	13-0071	Monrovia
		MORjos 060F (Josee)	10-0039	Blue Heron Farm
		Bailbelle (Tinkerbelle®)	12-0027	Bailey Nurseries
	S. pubescens ssp. *patula*	Miss Kim	13-0073	Monrovia
Villosae	*S. emodii*		09-0038	Hohenheim Gardens
	S. josikaea		09-0039	Hohenheim Gardens
	S. julianae		09-0057	Arborétum Mlyňany
	S. sweginzowii		11-0021	NBG Dublin
	S. tigerstedtii		09-0040	Hohenheim Gardens
	S. villosa		09-0061	Arborétum Mlyňany
			10-0020	Rogów Arboretum
	S. wolfii		09-0062	Mlynany Arboretum
			10-0021	Rogów Arboretum
	S. ×prestoniae	Miss Canada	13-0037	Briggs Nursery
		Miss Canada	13-0087	Monrovia
		Redwine	13-0088	Monrovia
	S. yunnanensis		09-0063	Arborétum Mlyňany

[z]Series designation based on phylogeny by Li et al. (2012).
[y]Individual taxon in *Syringa* based on current phylogeny (Li et al., 2012) and revisions (Chen et al., 2009).
[x]Accession number in research collection at Oregon State University, Corvallis, OR. Duplicate samples were clones and phenotypically identical.
[w]Container plants, seed, and leaf samples collected from the following sources: Arborétum Mlyňany (Slepcany, Slovakia), Bailey Nurseries (Yamhill, OR), Blue Heron Farm (Corvallis, OR), Briggs Nursery (Elma, WA), Carlton Plants (Dayton, OR), Dennis' 7 Dees Landscaping & Garden Centers (Portland, OR), Garland Nursery (Corvallis, OR), Heritage Seedlings & Liners (Salem, OR), Hohenheim Gardens (Stuttgart, Germany), Mason Hollow Nursery (Mason, NH), Monrovia (Dayton, OR), National Botanic Gardens [NBG Dublin (Glasnevin, Ireland)], Portland Nursery (Portland, OR), Rogów Arboretum (Rogów, Poland), Select Plus International Lilac Nursery (Mascouche, QC, Canada).

Each year, fresh pollen was collected and stored in small petri dishes over desiccant (Drierite; W.A. Hammond Drierite, Xenia, OH) in a refrigerator at 4 °C. Before pollination, open flowers were removed on all inflorescences and saved in glassine bags for pollen collection and reciprocal crosses. Individual flowers were emasculated before anthesis and pollinations were made in a glasshouse free of pollinators with day/night temperatures of 25/20 °C and a 16-h photoperiod. Each flower was pollinated using a brush two to three times postemasculation over consecutive days. Brushes were sterilized before and between pollinations using 70% ethanol. Incidences of self-pollination were tested by covering two inflorescences per plant with organza bags and shaking occasionally. Self-pollination can also occur if pollen is released during emasculation. Self-pollination during emasculation was tested by emasculating multiple inflorescences (200+ flowers) on two fertile parents (*S. vulgaris* 'Angel White' and *S. vulgaris* 'Ludwig Spaeth') and covering the inflorescences with organza

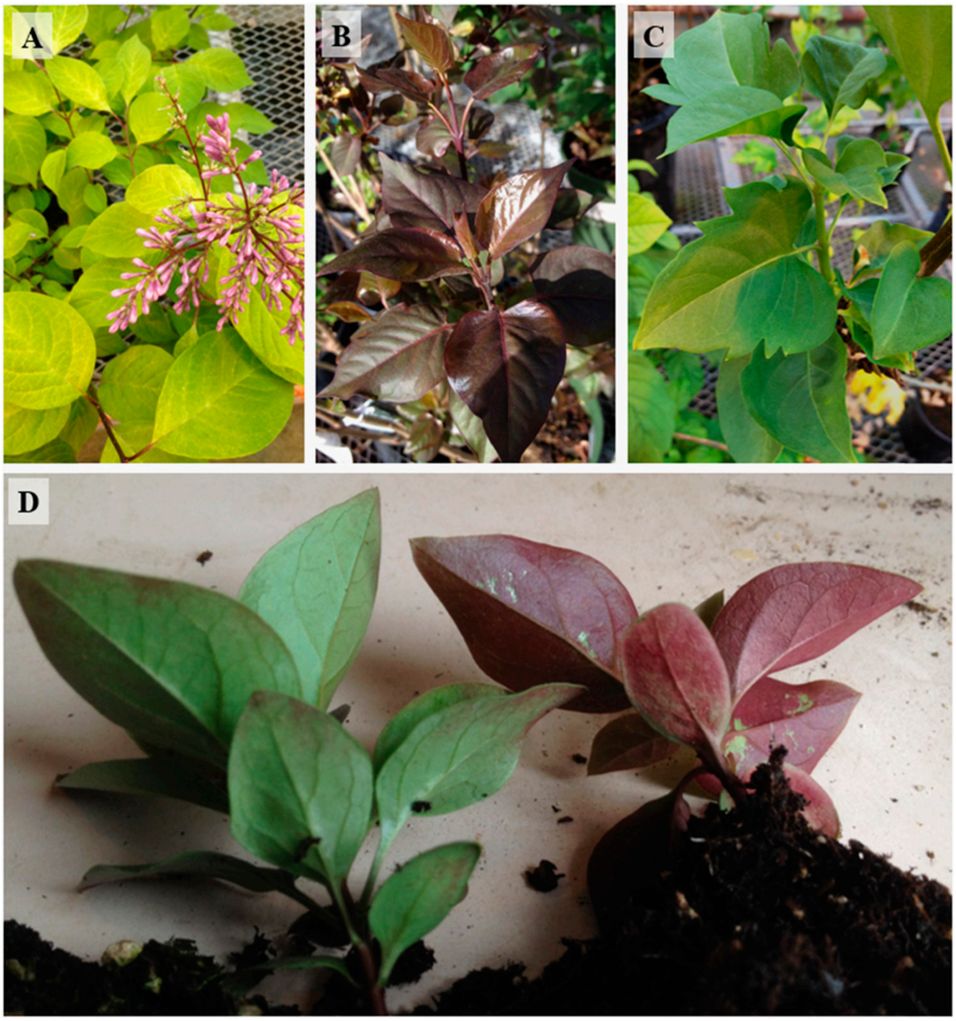

Fig. 1. Spring leaf color phenotypes in lilac breeding population: (**A**) yellow-green leaves of *Syringa emodii*, (**B**) purple leaves of *Syringa ×hyacinthiflora* 'Old Glory', (**C**) hybrid seedling (H2013-150-001) from the cross *Syringa vulgaris* 'President Grévy' x *Syringa vulgaris* 'Sensation', and (**D**) hybrid seedlings from the cross *Syringa vulgaris* 'Ludwig Spaeth' x *Syringa vulgaris* 'Angel White' segregating for abaxial leaf pigment.

bags. Developing fruit were counted throughout the summer and dry fruit were collected before dehiscence during fall. Data were collected on number of pollinated inflorescences, pollinated flowers, and developing fruit. During fall, seed were cleaned and counted before cold stratification during winter.

Seed germination. Seed were placed in plastic bags filled with moist stratification media consisting of half perlite (Supreme Perlite Co., Portland, OR) and half growing medium (Metro-Mix; Sun Gro Horticulture, Agawam, MA). Seed were cold-stratified for 10 weeks at 4 °C. After stratification, seed were sown in 1.3-L containers filled with the growing medium and treated once with copper hydroxide (Kocide 2000; DuPont, Wilmington, DE) at 0.3 mg·L^{-1}. For each cross, no more than 30 seed were sown per pot. Seedlings were germinated in a glasshouse under the conditions described previously. Data collected over winter included number of germinated seed, albino seedlings, and viable green seedlings.

In vitro germination. Capsules progressed from pollination to dehiscence over a 20- to 30-week period in the glasshouse. In 2013, observations of early fruit abortion at 6 weeks post-pollination in the interseries cross *S. oblata* x *S. pubescens* Bloomerang® Purple prompted an in vitro germination trial on a subset of developing fruit (Table 6). In subsequent years, fruit were allowed to dehisce early, and seed were sown according to the methods previously mentioned. For in vitro germination, interseries hybrid fruit from five crosses (Table 6) were collected 7 weeks after pollination. Green fruit were collected and immediately surface-sterilized by rinsing in a 70% ethanol solution for 30 s followed by a soak in a 6.15% (v/v) sodium hyporchlorite solution with several drops of surfactant (Tween 20; Acros Organics, Fair Lawn, NJ). Fruit were triple rinsed and temporarily stored in filter-sterilized, autoclaved water. Fruit were dissected in a sterile, laminar flow hood using a dissecting microscope. Green seed were removed from capsules into sterile petri dishes containing an aqueous solution of L-ascorbic acid at 25 mg·L^{-1} to reduce oxidation. Embryo extraction at this early stage proved too damaging to young tissues. Therefore, intact dissected seed were cultured on an embryo rescue medium.

Dissected seed were cultured on Monnier's medium according to the lilac embryo rescue protocol of Zhou et al. (2003) and incubated under standard culture conditions (24 ± 2 °C and a 16-h photoperiod of 60 μmol·m^{-2}·s^{-1} provided by cool-white fluorescent lamps). Seed were incubated on 10 mL of the embryo rescue medium in 150-mm culture tubes. Tubes were capped and sealed with paraffin film (parafilm; American National Can Co., Menasha, WI). A total of 161 seed were placed on the germination medium, representing five interseries crosses. Culture tubes were completely randomized and maintained in racks of 40 tubes. Germination was observed and recorded over 3 months. On germination, seedlings and callus were transferred to the shoot regeneration medium composed of Murashige and Skoog basal salts and vitamins, 5 μM BAP, 0.5 μM indole-3-butyric acid (IBA), 100 mg·L^{-1} *myo*-inositol, 100 mg·L^{-1} 2-(N-morpholino) ethanesulfonic acid (MES monohydrate), and 30 g·L^{-1} sucrose. The solution containing basal salts, vitamins, and hormones (Phytotechnology Laboratories, Shawnee Mission, KS) was adjusted to pH 5.8 and solidified with 7.5 g·L^{-1} agar (Sigma-Aldrich, St. Louis, MO).

Results and Discussion

A total of 3668 capsules were collected which produced 4890 seed and 2177 viable (nonalbino) hybrid seedlings. No fruit or seed resulted from emasculated/unpollinated flowers from the first self-pollination test. Six taxa produced seed from

Table 3. Intraspecific cross-compatibility within series *Pubescentes* and *Syringa* in lilac.

Series[z]	Female parent	Male parent	Pollinations (no.)[y]	Capsules (no.)[x]	Seed (no.)[w]	Germinated (no.)[v]
Pubescentes	*S. pubescens* Bloomerang® Purple	*S. pubescens* Josee	141	28	41	20
		S. pubescens 'Miss Kim'	175	1	1	0
		S. pubescens Tinkerbelle®	133	0	0	0
	S. pubescens Josee	*S. pubescens* Bloomerang® Purple	246	67	158	131
		S. pubescens 'Miss Kim'	137	4	5	0
		S. pubescens Tinkerbelle®	145	31	42	28
	S. pubescens 'Miss Kim'	*S. pubescens* Bloomerang® Purple	380	56	58	11[u]
		S. pubescens Josee	210	0	0	0
	S. pubescens Tinkerbelle®	*S. pubescens* Bloomerang® Purple	290	20	15	10
		S. pubescens Josee	199	0	0	0
		S. pubescens 'Miss Kim'	124	0	0	0
Syringa	*S. vulgaris* Tiny Dancer	*S. vulgaris* 'Angel White'	270	3	0	0
		S. vulgaris 'President Lincoln'	61	6	2	0
		S. vulgaris 'Sensation'	125	18	28	18
	S. vulgaris 'Angel White'	*S. vulgaris* 'Ludwig Spaeth'	353	153	204	55
	S. vulgaris Blue Skies®	S. *vulgaris* Tiny Dancer	100	81	160	61
		S. vulgaris 'President Grévy'	238	68	72	12
	S. vulgaris 'Lavender Lady'	*S. vulgaris* Tiny Dancer	176	75	93	47
	S. vulgaris 'Ludwig Spaeth'	*S. vulgaris* 'Angel White'	273	182	422	186
	S. vulgaris 'Prairie Petite'	*S. vulgaris* 'Sensation'	74	33	0	0
	S. vulgaris 'President Grévy'	S. *vulgaris* Tiny Dancer	304	3	2	0
		S. vulgaris 'Angel White'	182	4	3	0
		S. vulgaris 'President Lincoln'	81	0	0	0
		S. vulgaris 'Sensation'	240	100	107	1
	S. vulgaris 'President Lincoln'	*S. vulgaris* 'Angel White'	135	27	23	12
		S. vulgaris 'President Grévy'	126	0	0	0
	S. vulgaris 'Sensation'	*S. vulgaris* Tiny Dancer	95	12	14	20
		S. vulgaris 'President Grévy'	376	16	13	0

[z]Intraspecific crosses within two series of lilac: *Pubescentes* and *Syringa* (Li et al., 2012).
[y]Number of emasculated flowers pollinated.
[x]Number of capsules formed from controlled crosses.
[w]Number of seed produced from controlled crosses.
[v]Number of seed germinated.
[u]All nonviable albino seedlings.

the nonemasculated, self-pollination tests, but only two taxa produced viable seedlings. *Syringa pubescens* Tinkerbelle® self-pollinations yielded 36 seed and 20 viable seedlings. *Syringa meyeri* 'Palabin' self-pollinations yielded one seed and one viable seedling. The following taxa self-pollinations yielded three or fewer seed and no viable seedlings: *S.* ×*hyacinthiflora* 'Old Glory', *S. vulgaris* Blue Skies®, *S. vulgaris* 'Sensation', and *S. vulgaris* Tiny Dancer. Because each self-pollination test was performed on more than 200 flowers per taxon, incidences of self-pollinations were determined to be negligible during controlled crosses.

Viable seedlings across all taxa exhibited a quiescent phase of vegetative growth during their first year. During this period, seedlings produced few sets of leaves while they developed an expansive root system. In following years, these seedlings exhibited large flushes of vegetative growth. Few phenotypic observations could be made on young seedlings, except for variation in form and leaf pigments. All hybrid seedlings exhibited entire margins except for a single seedling from the cross between the double-flowered *S. vulgaris* 'President Grévy' and picotee-flowered *S. vulgaris* 'Sensation' (Fig. 1C). This hybrid (H2013-150-001) had leaves with irregular sinuses in its second and third years of growth. In series *Syringa*, seedlings of parents with lavender or dark purple flowers had a range of abaxial foliar pigment levels. Seedlings with the darkest pigment were from crosses with the purple-leaved *S.* ×*hyacinthiflora* 'Old Glory' (Fig. 1B). The widest range of color segregation was observed in *S. vulgaris* 'Ludwig Spaeth' x *S. vulgaris* 'Angel White' where leaf color ranged from green to dark purple (Fig. 1D). In series *Pubescentes*, one parent, *S. pubescens* ssp. *patula* 'Miss Kim', produced only nonviable, albino progeny which failed to survive germination.

Intraspecific hybridization. Within series *Pubescentes*, a total of 2180 pollinations resulted in an average of 17.18 ± 11.75 viable seedlings per cross. However, only four crosses yielded viable seedlings of the 11 attempted. The most prolific cross was between two remontant taxa, *S. pubescens* Josee × *S. pubescens* Bloomerang® Purple, which produced 131 viable seedlings at 0.53 seedlings per pollinated flower (Table 3). The reciprocal cross produced 20 viable seedlings at 0.14 seedlings per pollinated flower (Table 3). *Syringa pubescens* Josee was also an effective seed parent in crosses with *S. pubescens* Tinkerbelle®, yielding 28 viable seedlings at 0.19 seedlings per pollinated flower (Table 3). The fewest viable seedlings were produced from *S. pubescens* Tinkerbelle® x *S. pubescens*

Table 4. Interspecific cross-compatibility within series *Pubescentes*, *Syringa*, and *Villosae* in lilac.

Series[z]	Female parent	Male parent	Pollinations (no.)[y]	Capsules (no.)[x]	Seed (no.)[w]	Germinated (no.)[v]
Pubescentes	*S. meyeri* 'Palabin'	*S. pubescens* Bloomerang® Purple	239	144	398	278
		S. pubescens Josee	706	47	47	19
		S. pubescens 'Miss Kim'	522	24	39	0
		S. pubescens Tinkerbelle®	206	83	155	134
	S. pubescens Josee	*S. meyeri* 'Palabin'	122	38	82	63
	S. pubescens 'Miss Kim'	*S. meyeri* 'Palabin'	601	417	900	149[u]
	S. pubescens Tinkerbelle®	*S. meyeri* 'Palabin'	253	64	58	31
Syringa	*S. oblata*	*S. vulgaris* Tiny Dancer	92	13	14	10
		S. vulgaris 'Lavender Lady'	162	0	0	0
	S. *oblata* var. *alba*	*S. vulgaris* Tiny Dancer	208	53	75	47
		S. vulgaris 'President Lincoln'	226	0	0	0
	S. vulgaris Tiny Dancer	*S. oblata*	175	17	10	8
		S. *oblata* var. *alba*	170	59	75	68
		S. ×hyacinthiflora 'Old Glory'	166	96	172	160
		S. ×hyacinthiflora 'Pocahontas'	32	6	0	0
	S. vulgaris 'Agincourt Beauty'	*S. ×hyacinthiflora* 'Old Glory'	116	56	81	6
	S. vulgaris Blue Skies®	S. *oblata* var. *alba*	103	5	5	4
		S. ×hyacinthiflora 'Betsy Ross'	135	103	214	191
	S. vulgaris 'Lavender Lady'	*S. oblata*	131	48	67	49
		S. *oblata* var. *alba*	155	6	2	0
	S. vulgaris 'Prairie Petite'	*S. ×hyacinthiflora* 'Old Glory'	20	0	0	0
	S. vulgaris 'President Grévy'	*S. ×hyacinthiflora* 'Old Glory'	176	59	76	0
	S. vulgaris 'Sensation'	*S. ×hyacinthiflora* 'Old Glory'	173	73	0	0
	S. ×hyacinthiflora 'Betsy Ross'	*S. oblata*	79	2	2	1
		S. *oblata* var. *alba*	112	8	8	5
	S. ×hyacinthiflora 'Maiden's Blush'	*S. oblata*	164	11	15	13
	S. ×hyacinthiflora 'Old Glory'	*S. oblata*	234	70	154	125
		S. *oblata* var. *alba*	290	0	0	0
		S. *vulgaris* Tiny Dancer	122	29	42	37
		S. vulgaris 'Angel White'	195	57	95	37
Villosae	*S. emodii*	*S. ×prestoniae* 'Miss Canada'	240	0	0	0
		S. villosa	213	0	0	0
		S. wolfii	309	0	0	0
		S. yunnanensis	243	0	0	0
	S. julianae	*S. ×prestoniae* 'Miss Canada'	255	69	122	100
	S. villosa	*S. ×prestoniae* 'Miss Canada'	181	0	0	0
		S. emodii	169	0	0	0
		S. wolfii	179	0	0	0
	S. wolfii	*S. ×prestoniae* 'Miss Canada'	175	0	0	0
		S. emodii	215	31	25	24
		S. villosa	178	11	14	6
	S. yunnanensis	*S. julianae*	177	0	0	0
		S. ×prestoniae 'Miss Canada'	209	0	0	0
	S. ×prestoniae 'Miss Canada'	*S. wolfii*	254	0	0	0

[z]Interspecific crosses within three series of lilac: *Pubescentes*, *Syringa*, and *Villosae* (Li et al., 2012).
[y]Number of emasculated flowers pollinated.
[x]Number of capsules formed from controlled crosses.
[w]Number of seed produced from controlled crosses.
[v]Number of seed germinated.
[u]Nonviable albino seedlings produced.

Bloomerang® with only 10 viable seedlings produced at 0.03 seedlings per pollinated flower (Table 3).

Within series *Syringa*, a total of 3209 pollinations resulted in an average of 24.24 ± 11.28 viable seedlings per cross. Of the 17 crosses attempted, eight yielded viable seedlings. The most prolific was *S. vulgaris* 'Ludwig Spaeth' x *S. vulgaris* 'Angel White' producing 186 seedlings at 0.68 seedlings per pollinated flower (Table 3). Of the dwarfs, *S. vulgaris* 'Prairie Petite' was the smallest and slowest growing, producing few inflorescences each year. One cross performed with *S. vulgaris* 'Prairie Petite' used 74 pollinations with *S. vulgaris* 'Sensation' and yielded 33 capsules but no seed (Table 3). The dwarf *S. vulgaris* Tiny Dancer was

Table 5. Interseries cross-compatibility among series *Pubescentes*, *Syringa*, and *Villosae* in lilac.

Interseries cross[z]	Female parent	Male parent	Pollinations (no.)[y]	Capsules (no.)[x]	Seed (no.)[w]	Germinated (no.)[v]
Pubescentes × *Villosae*	*S. pubescens* Bloomerang® Purple	*S. ×prestoniae* 'Miss Canada'	482	17	8	0
	S. pubescens Josee	*S. ×prestoniae* 'Miss Canada'	500	65	49	0
		S. ×prestoniae 'Redwine'	150	1	1	0
Villosae × *Pubescentes*	*S. emodii*	*S. pubescens* Bloomerang® Dark Purple	82	21	14	0
		S. pubescens Bloomerang® Purple	97	0	0	0
	S. josikaea	*S. meyeri* 'Palabin'	58	0	0	0
		S. pubescens Josee	149	6	0	0
		S. pubescens Tinkerbelle®	135	10	0	0
	S. julianae	*S. pubescens* Bloomerang® Dark Purple	64	16	0	0
	S. sweginzowii	*S. pubescens* Bloomerang® Dark Purple	237	22	0	0
	S. tigerstedii	*S. pubescens* Bloomerang® Dark Purple	130	12	0	0
	S. villosa	*S. pubescens* Bloomerang® Dark Purple	219	0	0	0
	S. wolfii	*S. pubescens* Bloomerang® Purple	176	0	0	0
	S. yunnanensis	*S. pubescens* Bloomerang® Dark Purple	163	0	0	0
	S. ×prestoniae 'Miss Canada'	*S. pubescens* Bloomerang® Purple	425	80	73	0
	S. ×prestoniae 'Redwine'	*S. pubescens* Bloomerang® Purple	617	56	44	0
		S. pubescens Josee	602	174	129	0
Pubescentes × *Syringa*	*S. meyeri* 'Palabin'	*S. oblata*	179	10	6	0
		S. vulgaris 'Angel White'	91	0	0	0
		S. vulgaris 'Sensation'	197	55	39	0
	S. pubescens Bloomerang® Purple	*S. vulgaris* 'Ludwig Spaeth'	2,098	31	21	3[u]
	S. pubescens Josee	*S. oblata*	138	60	77	0
		S. oblata var. *alba*	329	1	1	0
	S. pubescens 'Miss Kim'	*S. oblata*	223	0	0	0
		S. vulgaris 'President Grévy'	408	0	0	0
	S. pubescens Tinkerbelle®	*S. oblata*	271	0	0	0
Syringa × *Pubescentes*	*S. oblata*	*S. pubescens* Bloomerang® Purple	547	238	0	0
	S. vulgaris 'Ludwig Spaeth'	*S. pubescens* Bloomerang® Purple	2,206	27	18	0
	S. vulgaris 'President Grévy'	*S. pubescens* Bloomerang® Purple	68	27	0	0
	S. ×hyacinthiflora 'Old Glory'	*S. pubescens* Bloomerang® Purple	35	0	0	0
Syringa × *Villosae*	*S. ×hyacinthiflora* 'Old Glory'	*S. villosa*	176	46	0	0
		S. wolfii	248	1	0	0
		S. yunnanensis	153	0	0	0
		S. ×prestoniae 'Miss Canada'	305	0	0	0
	S. vulgaris 'President Grévy'	*S. ×prestoniae* 'Miss Canada'	22	0	0	0
	S. vulgaris 'Sensation'	*S. julianae*	172	0	0	0
		S. villosa	142	0	0	0
		S. wolfii	149	0	0	0
		S. ×prestoniae 'Miss Canada'	232	5	0	0
Villosae × *Syringa*	*S. ×prestoniae* 'Miss Canada'	*S. vulgaris* 'Sensation'	295	0	0	0
	S. wolfii	*S. vulgaris* Blue Skies®	122	0	0	0

[z]Interseries crosses representing six reciprocal combinations of three series of lilac: *Pubescentes*, *Syringa*, and *Villosae* (Li et al., 2012).
[y]Number of emasculated flowers pollinated.
[x]Number of capsules formed from controlled crosses.
[w]Number of seed produced from controlled crosses.
[v]Number of seed germinated.
[u]Attempted vitro germination of seed on Monnier's medium according to Zhou et al. (2003); seedlings did not survive germination.

used successfully as both a seed and pollen parent in intraspecific crosses. As a seed parent, *S. vulgaris* Tiny Dancer was compatible with *S. vulgaris* 'Sensation' at 0.14 seedlings per pollinated flower, whereas the reciprocal cross yielded 0.21 seedlings per pollinated flower. As a pollen parent, *S. vulgaris* Tiny Dancer was compatible with *S. vulgaris* Blue Skies® at 0.61 seedlings per pollinated flower and *S. vulgaris* 'Lavender Lady' at 0.27 seedlings per pollinated flower (Table 3). *Syringa vulgaris* 'President Grévy' had few successful crosses. As a seed parent, 807 intraspecific pollinations were performed with four taxa, and only one seedling was produced from a cross with *S. vulgaris* 'Sensation' (Table 3). As a pollen parent, 740 pollinations were performed with *S. vulgaris* 'President Grévy' on three taxa. Only *S. vulgaris* Blue Skies® proved an effective seed parent, with 12 seedlings produced at 0.05 seedlings per pollination (Table 3).

Interspecific hybridization. Within series *Pubescentes*, interspecific crosses were performed between cultivars of *S. pubescens* and *S. meyeri* 'Palabin'. A total of 2649 pollinations

Table 6. Attempted pollinations, recovered seed, and in vitro germination of interseries lilac hybrids in 2013. All seed collected from green capsules and cultured on cultured on Monnier's medium as described by Zhou et al. (2003).

Female parent	Male parent	Pollinated flowers (no.)	Seed (no.)	Germinated (no.)
S. vulgaris 'Ludwig Spaeth'	*S. pubescens* Bloomerang® Purple	2,206	18	0
S. oblata	*S. pubescens* Bloomerang® Purple	547	0[z]	0
S. meyeri 'Palabin'	*S. oblata*	179	6	0
	S. vulgaris 'Angel White'	91	0	0
	S. vulgaris 'Sensation'	197	39	0
S. pubescens 'Miss Kim'	*S. oblata*	223	0	0
	S. vulgaris 'President Grévy'	408	0	0
S. pubescens Josee	*S. oblata*	138	77	0
S. pubescens Bloomerang® Purple	*S. vulgaris* 'Ludwig Spaeth'	2,098	21	3[y]

[z]Early abortion of 238 fruit occurred 6 weeks postpollination.
[y]Radicle, hypocotyl, and cotyledons emerged; seedlings failed to grow postgermination and tissues subsequently converted to callus.

resulted in an average of 96.29 ± 37.12 viable seedlings per cross (Table 4). Of the seven crosses, two failed to produce viable seedlings. As a seed parent, *S. pubescens* 'Miss Kim' yielded 149 nonviable, albino seedlings, whereas reciprocal crosses yielded no seedlings after 522 pollinations (Table 4). The most prolific cross, *S. meyeri* 'Palabin' x *S. pubescens* Bloomerang® Purple, yielded 278 seedlings at 1.16 seedlings per pollinated flower (Table 4).

Within series *Syringa*, interspecific crosses were performed among taxa of *S. vulgaris*, *S. ×hyacinthiflora*, and *S. oblata*. A total of 3518 pollinations resulted in an average of 31.71 ± 10.93 viable seedlings per cross (Table 4). Of the 24 crosses, 15 resulted in viable seedlings. The most prolific cross was *S. vulgaris* Blue Skies® x *S. ×hyacinthiflora* 'Betsy Ross' producing 1.41 seedlings per pollinated flower (Table 4). Although *S. oblata* was successful in a number of interspecific crosses, the white-flowered *S. oblata* var. *alba* produced large seedling populations only in crosses with *S. vulgaris* Tiny Dancer. This cross produced 68 viable seedlings at 0.40 seedlings per pollination, whereas the reciprocal cross produced 47 seedlings at 0.23 seedlings per pollination (Table 4).

Not surprisingly, cultivars of *S. ×hyacinthiflora*, crossed successfully with cultivars of *S. vulgaris* and wild-type *S. oblata*. Crosses with *S. ×hyacinthiflora* 'Old Glory' were of interest for future breeding because of the lack of flower and form diversity in purple-leaved cultivars. *Syringa ×hyacinthiflora* 'Old Glory' proved a successful seed parent in crosses with white-flowered *S. vulgaris* 'Angel White', yielding 37 seedlings at 0.19 seedlings per pollinated flower (Table 4). Despite 176 pollinations and 76 recovered seed, *S. ×hyacinthiflora* 'Old Glory' produced no viable seedlings with the double-flowered *S. vulgaris* 'President Grévy'. When crossed with the dwarf *S. vulgaris* Tiny Dancer, *S. ×hyacinthiflora* 'Old Glory' proved an efficient seed parent producing 37 seedlings at 0.30 seedlings per pollination. The reciprocal cross was even more efficient, yielding 160 seedlings at 0.96 seedlings per pollination (Table 4).

Within series *Villosae*, only three of 14 crosses produced seedlings. A total of 2997 pollinations yielded an average of 9.29 ± 7.19 seedlings per cross combination (Table 4). The most prolific cross was *S. julianae* x *S. ×prestoniae* 'Miss Canada' which produced 100 viable seedlings at 0.48 seedlings per pollinated flower (Table 4). In addition, *S. julianae* had some of the largest flowers in series *Villosae* with a fragrance reminiscent of *S. vulgaris*. The only other seed parent to produce viable seedlings in interspecific crosses in series *Villosae* was *S. wolfii*. The cross between *S. wolfii* and the yellow-leaved *S. emodii* (Fig. 1A) produced 24 seedlings at 0.11 seedlings per pollinated flower (Table 4). Only six seedlings resulted from crosses between *S. wolfii* and *S. villosa* yielding 0.03 seedlings per pollinated flower (Table 4).

Interseries hybridization. Interseries crosses proved the most challenging because of differences in bloom time. It took 3 years to complete a range of interseries crosses. A typical lilac will bloom for 6 weeks in an average season with reliable patterns of bloom across series and species (Fiala, 1988). Our observations agreed with Fiala (1988) with members of series *Syringa* blooming first in spring, followed by series *Pubescentes* in late spring to early summer and series *Villosae* in early to midsummer. During the first year, pollen was collected from early-blooming plants and the sequence of blooming was noted across all taxa. Bloom data were used to design reciprocal interseries crosses over the following 2 years where temperature was altered to hasten or slow bloom. Earlier bloom times were induced in late-blooming taxa using a heated glasshouse. Delayed bloom times were induced in early-blooming taxa using a walk-in cooler.

For series *Pubescentes*, *Syringa*, and *Villosae*, there were six possible combinations of interseries crosses (Table 5). A total of 41 crosses were performed across these six combinations representing 13,092 pollinations (Table 5). No viable seedlings were recovered although some crosses produced capsules and seed (Table 5). Across all the interseries combinations, 975 capsules were recovered which produced 480 seed. Seed-producing crosses could provide a foundation for future studies on embryo abortion and embryo rescue.

Interseries crosses between *Pubescentes* and *Villosae* included seven crosses that produced capsules and seed. These crosses included *S. emodii* and cultivars of *S. pubescens* and *S. ×prestoniae* (Table 5). Capsules and seed were produced when taxa in *Pubescentes* and *Villosae* were used as seed parents. The most prolific cross was *S. ×prestoniae* 'Redwine' × *S. pubescens* Josee which produced 129 seed from 174 capsules after 602 pollinations (Table 5).

Interseries crosses between *Pubescentes* and *Syringa* included five crosses that produced capsules and seed. Only one cross produced seed with series *Syringa* as a seed parent, *S. vulgaris* 'Ludwig Spaeth' x *S. pubescens* Bloomerang®. This cross resulted in 27 capsules and 18 seed after 2206 pollinations (Table 5). Four crosses produced seed using series *Pubescentes* as a seed parent. The cross *S. oblata* x *S. pubescens* Bloomerang® Purple produced the most capsules of any interseries cross at

238 capsules from 547 pollinations. However, these capsules aborted 6 weeks after pollination, unlike most interseries capsules which persisted for the 20- to 30-week development period. The most prolific cross between series *Pubescentes* and *Syringa* was *S. pubescens* Josee x *S. oblata*, yielding 77 seed from 138 pollinations at 0.56 seed per pollination (Table 5).

No interseries cross between series *Syringa* and *Villosae* produced seed-filled capsules. Of the 2016 pollinations, capsules were produced from three crosses: *S. ×hyacinthiflora* 'Old Glory' x *S. villosa*, *S. ×hyacinthiflora* 'Old Glory' x *S. wolfii*, and *S. vulgaris* 'Sensation' x *S. ×prestoniae* 'Miss Canada' (Table 5). The most prolific cross was *S. ×hyacinthiflora* 'Old Glory' x *S. villosa* which yielded 46 capsules from 176 pollinations (Table 5).

In vitro germination. A preliminary trial extracting open-pollinated lilac seed and embryos from green capsules revealed the difficulty of embryo extraction at this young stage. Oxidation of the young seed progressed rapidly during excision and phenolics proved damaging when immature seed were cultured in vitro. Excising seed while submerged in an antioxidant solution reduced oxidation and allowed extraction of undamaged green seed. Immature seed obtained from interseries crosses in 2013 had low germination in vitro on Monnier's medium (Table 6). Most seed failed to germinate and eventually became necrotic. Of the 161 seed cultured in vitro, only three germinated, all from the cross *S. pubescens* 'Penda' Bloomerang® Purple x *S. vulgaris* 'Ludwig Spaeth' (Table 6). Seedlings failed to grow post germination and tissues, including cotyledons, subsequently converted to callus. This result may be due to lack of proper transfer media postgermination or lack of proper combination of genotype and in vitro germination medium. Surprisingly, Zhou et al. (2003) did not report the genotype used in their protocol. Further research will be necessary to design protocols for in vitro seed germination and embryo rescue in lilac. Callus obtained from cotyledons could provide source material for somatic embryogenesis in future studies, as demonstrated by Liu et al. (2013).

Though interseries crosses and in vitro germination failed to achieve hybrids, the quantity of seed produced combined with several seed that germinated in vitro provides evidence that future work on wide hybridization in lilacs may prove fruitful. Anatomical studies have shown that low-germination lilac seed contain embryos that progress to walking stick stage before abortion (Chen et al., 2012). This study lists individual cross combinations between series *Pubescentes* and *Villosae*, as well as *Pubescentes* and *Syringa*, which produced large numbers of seed (Table 5). In addition, current research at North Dakota State University also observed fruit development in interseries crosses between series *Villosae* and the tree lilacs in *Ligustrina* that persisted well into the summer before fruit abortion (N.G. Maren, personal communication).

This study represents a comprehensive investigation of lilac cross-compatibility. Intraspecific and interspecific crosses produced hybrid progeny from a diverse set of crosses. The resulting seedlings will be used to study phenotypic segregation of flower traits such as color, double flowers, picotee petals, and remontancy. Seedlings from crosses with *S. vulgaris* Tiny Dancer will be used to study segregation of the dwarf phenotype. Seedlings from crosses *Syringa ×hyacinthiflora* 'Old Glory' and *S. emodii* will be used to study segregation of the purple- and yellow-leaved phenotypes, respectively. Selections among hybrid seedlings may identify novel combinations of traits such as purple-leaved dwarfs, double-flowered dwarfs, or double-picotee flowers.

Cross-incompatibility may be due to differences in genome size and ploidy level. Future evaluation of genome size and ploidy among taxa may provide insight into cross-compatibility in the current study. Cytological studies describe lilacs to be primarily diploids (Darlington and Wylie, 1956) with holoploid genome sizes near 2.5 pg (Olszewska and Osiecka, 1984; Siljak-Yakovlev et al., 2010). Cross-incompatibility can also be a function of pollination biology. Self-incompatibility systems have been discovered in related genera (*Phillyrea*, *Fraxinus*, and *Olea*) and sporophytic cross-incompatibility systems with *S*-allele dominance relationships have been discovered in cultivars of *Olea* (Breton et al., 2014; Collani et al., 2012; Koubouris et al., 2014; Saumitou-Laprade et al., 2017; Vernet et al., 2016). Future studies investigating rates of gametophytic/sporophytic incompatibility and unreduced gametes may provide insights into cross-compatibility. Environmental conditions have also been shown to affect seed development in lilacs (Junttila, 1973), and the current study may provide crosses useful for determining optimum greenhouse temperatures for pollination.

While many intraspecific and interspecific crosses were successful, no interseries crosses yielded viable seedlings. Some interseries crosses did, however, produce capsules and seed. A preliminary in vitro germination trial yielded low germination percentage and callus production. These results provide evidence that interseries hybrids among series *Syringa*, *Pubescentes*, and *Villosae* may be possible. Interseries seed development in hybrids with *Ligustrina* have also shown promise. In future research, seed-producing interseries crosses could be repeated and anatomical studies on embryo development, similar to Chen et al. (2012), may yield important information for targeting future embryo rescue efforts. Open-pollinated seed could be used to identify suitable culture media. Tissue culture and embryo rescue protocols are highly genotype-specific; therefore, cross-specific embryo rescue and embryogenic callus media could be fine-tuned for interseries hybrids that produce viable embryos early in seed development. Recovery of interseries hybrids in lilac will likely prove difficult. However, the current study in combination with other breeding and tissue culture studies provides a foundation for development of novel hybrid lilacs. For a group of ornamental shrubs and trees that have been bred for nearly 500 years, there are still new horizons for breeders to pursue in modern lilac breeding.

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