Sowing Green Seed Without Stratification Does Not Shorten Juvenility or Increase Plant Size in Common Lilac (*Syringa vulgaris*)

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Abstract. Common lilac is an important flowering shrub that accounts for ≈\$20 million of sales in the U.S. nursery industry. Cultivar improvement in common lilac has been ongoing for centuries, yet little research has focused on shortening the multiple-year juvenility period for lilacs and the subsequent time required between breeding cycles. The practice of direct-sowing of immature “green” seed has been shown to reduce juvenility in some woody plants, but it has not been reported for common lilac. This study investigated the effects of seed maturity [weeks after pollination (WAP)], pregermination seed treatment (direct-sown vs. cold-stratified), and postgermination seedling chilling on the germination percentage, subsequent plant growth, and time to flower on lilac seedlings. All seedlings were derived from the female parent ‘Ludwig Spaeth’ and the male parent ‘Angel White’. Seeds harvested at 15 and 20 WAP resulted in 58% (SD ± 9.9%) and 80% (SD ± 9.0%) germination, respectively, which were similar to that of dry seed collected at 20 WAP with stratification (62% ± 4.2%). Seedlings from the green seed collected at 15 and 20 WAP were also approximately three-times taller than those of dry seed groups DS1, DS2, and DS3 after the first growing season. Over the next two growing seasons, there were no differences in seedling height across all treatments. Flowering occurred at the beginning of the fourth season and without differences among treatments. These results indicate that the collection and direct sowing of immature, green seed can be used to successfully grow lilac seedlings, but that they do not reduce the juvenility period. However, this method can provide more vegetative growth in year one to observe early vegetative traits such as leaf color, and it can provide more material for DNA extraction to support molecular research.

Common lilac (*Syringa vulgaris*) is a clonally propagated woody shrub that has been the subject of intense breeding for centuries due to its fragrant, colorful spring

blooms (Fiala and Vrugtman, 2008). The majority of species originated in Asia, with only *S. vulgaris* and *S. josikaea* originating in Europe (Fiala, 1988). The center of diversity of common lilac lies in the Balkans, and native populations can be found throughout southeastern Europe (Fiala, 1988). The impact of lilacs on the U.S. nursery industry is substantial, with nearly \$20 million in revenue generated from more than 1.8 million plants sold in 2014 (USDA, 2016). Still, improvements remain possible, such as improved disease resistance, reblooming, and combining other ornamental traits of signif-

A major limiting factor involved in woody plant breeding is the length of time between successive generations. Juvenility in woody plants is a natural process that prevents flowering in seedlings. Woody plants in nature produce vegetative growth for years under competition before diverting resources

to fruit and seed production (van Nocker and Gardiner, 2014). Lilacs typically begin sporadic flowering 3 years after germination, with consistent flowering after 4 years. Breeders have several techniques available for circumventing this mechanism that mostly focus on the cultural conditions after germination. One method is to provide optimal growing conditions to promote vigorous, vegetative growth. Apple breeders growing seedlings under optimal conditions have reduced juvenility to 10 months compared with 5 years for field-grown seedlings (Aldwinckle, 1975). Plant growth regulators (PGRs) can promote early flowering, although this approach has proven highly variable and has not been widely adopted for reducing juvenility (Zimmerman et al., 1985). For large trees with longer juvenility periods, combinations of PGR applications, root restriction, and girdling have been proven effective for reducing juvenility (Philipson, 1996; Snowball et al., 1994). When seedlings reach maturity, forcing is a cultural method that can be used to trigger vegetative and floral development in lilacs using high temperatures from 37 °C in November or 15 °C in March (Jędrzejuk et al., 2016b). However, high temperatures required for forcing often degrades pollen and ovules, making this technique problematic for breeding (Jędrzejuk et al., 2016b). Recent research has also proved that low-temperature forcing reduces oxidative stress in lilac flowers, which may be useful for lilac breeders (Jędrzejuk et al., 2016a).

Expediting seed germination is another option for shortening the generation time of woody plants. Efforts to overcome lengthy periods of seed dormancy have proven effective, including “green” seed germination, embryo culture, bioactive gibberellic acid treatments, and nitric oxide treatments (Bethke et al., 2007; Bridgen, 1994; Shen et al., 2011; West et al., 2014; van Nocker and Gardiner, 2014). The simplest is early or “green” seed collection, which has been effective for seed germination in several woody plant taxa, including *Tilia americana* (Dirr and Heuser, 2006) and *Syringa reticulata* (West et al., 2014). Seed development and the depth of physiological dormancy vary in lilacs, partly because of genetic variations and environmental conditions such as temperature postpollination (Junttila, 1973b). In tree lilac, *S. reticulata*, seeds were determined to be fully mature and capable of germinating as the green capsule color began to fade (West et al., 2014). Germination was optimized in this study by collecting capsules at 1-week intervals just as the green color began to fade in early fall. Germination diminished precipitously as moisture content was lost (West et al., 2014).

In a previous study of cross-compatibility among lilac cultivars (Lattier and Contreras, 2017), germinated seedlings from cold-stratified seed were observed to have a quiescent phase during their first year when vegetative growth was limited, but the seedling developed a large root system (Fig. 1A).

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Seedlings produced a large flush of vegetative growth in their second year (J. Lattier, personal observation). In 2014, a preliminary trial of immature seed germination was conducted. Predehiscid green, yellow-green, and yellow capsules were collected in summer from a random assortment of lilac parents. Seeds were direct-sown in containers (Fig. 1B) and in petri dishes with moistened filter paper (Fig. 1C). Only seeds excised from yellow-green and yellow capsules germinated. Direct-sown seeds grew to their quiescent phase in a glasshouse before being moved to an unheated polyhouse for winter dormancy. In spring, these seedlings produced a large flush of vegetative growth and quickly achieved the same size as stratified seedlings from the previous year (J. Lattier, personal observation). These preliminary results provided a proof-of-concept that germinating immature seed may be a means of reducing generation time for lilac breeders.

This study aimed to 1) determine the optimum germination treatment to overcome the quiescent phase before the first year of growth, and 2) determine if germination treatments improved growth and reduced juvenility in common lilac.

Materials and Methods

Plant materials. In Spring 2015, two lilac cultivars were selected based on their cross-compatibility reported by a previous study (Lattier and Contreras, 2017). *Syringa vulgaris* ‘Ludwig Spaeth’ (10-0042) and *S. vulgaris* ‘Angel White’ (10-0043) were acquired from Blue Heron Farms in Corvallis, OR. In early spring, before anthesis, parent cultivars were placed in a glasshouse, kept free of pollinators, and grown under day/night set temperatures of 25 °C/20 °C and a 16-h photoperiod using 400-W high-pressure sodium lamps. The pollen parent, *S. vulgaris* ‘Angel White’, was moved into the heated glasshouse $\approx$ 2 weeks before the seed parent, *S. vulgaris* ‘Ludwig Spaeth’, to hasten flower development for pollen collection.

As flowers of *S. vulgaris* ‘Angel White’ reached anthesis, fresh pollen was collected and stored in 50-mm-diameter petri dishes over desiccant (Drierite; W.A. Hammond Drierite Co., Ltd., Xenia, OH) in a refrigerator at 4 °C. Two to four anthers from each flower were collected; no petal tissue was stored with pollen. Before pollination, open flowers on *S. vulgaris* ‘Ludwig Spaeth’ were removed from all inflorescences. Individual flowers on multiple inflorescences were emasculated before anthesis. Each flower was pollinated using a small paintbrush two to three times postemasculature over consecutive days. All inflorescences were marked with jewelry tags and labeled with the cross-combination, date, and number of flowers pollinated. Over the course of a single day, more than 600 flowers were pollinated on 13 inflorescences; all other inflorescences were removed.

Germination experiment. Developing capsules were selected randomly for collection at 5, 10, 15, and 20 WAP. At each WAP interval, the seed color (which corresponded with the capsule color) and phase of seed development (turgid green seed or dry dehiscid seed) data were recorded (Table 1). Each predehiscid, immature capsule collected (Fig. 2A) was immediately surface-sterilized by soaking in 70% ethanol for 1 min (Fig. 2B). Capsules were placed in a sterile sieve and thoroughly rinsed with sterile water (Fig. 2C). Capsules were stored in vials of sterile water until seed extraction. Seeds were carefully excised on sterile paper plates using scalpel and forceps (Fig. 2D). Excised seeds were stored in sterile, distilled water until sown (Fig. 2E). Dehiscid, mature capsules were collected, and dry seed was direct-sown or allowed to completely dry before being subjected to cold stratification (Fig. 2F). For each treatment, 60 seeds were divided into four lots of 15 seeds and sown in 15.2-cm-diameter pots filled with a peat-based potting media (Metro-Mix 840pc Professional Growing Mix; Sun Gro Horticulture, Agawam, MA). Seeds were sown

$\approx$ 1.3 cm below the surface of the media, and pots were completely randomized in a glasshouse under the environmental conditions described. For each WAP interval, the process of capsule collection, seed excision, and sowing occurred during 1 d.

At 20 WAP, half of the capsules on *S. vulgaris* ‘Ludwig Spaeth’ were dehiscid and half were still immature and predehiscid. Two experimental groups were direct-sown at 20 WAP from these two types of capsules, and the remaining dehiscid capsules were collected in bulk (Table 1). This concluded the sequential removal of capsules from the seed parent, leaving four immature, green seed (GS) treatment groups (GS1, GS2, GS3, GS4) and one mature, dry seed (DS) group (DS1) (Table 1). A third experimental group (DS2) was created from the 20 WAP bulk seed to compare germination of direct-sown seed (DS1) with germination of cold-stratified seed (Table 1). In the DS2 group, four repetitions of 15 seeds each were sown in containers as described and placed in a cooler at 4 °C for 10 weeks before being returned to the glasshouse. Plants were germinated and grown under glasshouse conditions for the remainder of the winter. Germination for each treatment group was recorded after 1 month (Fig. 3), meeting the prescribed 21-d requirement for lilac germination tests (Isely and Everson, 1965; International Seed Testing Association, 1966).

Postgermination experiment. Treatments groups that were direct-sown and produced viable seedlings (GS2, GS3, GS4, DS1) were transplanted to 0.9-L containers and grown in a glasshouse through late summer and early Fall 2015. Then, they were placed in an unheated polyhouse and allowed to go dormant for the winter. The cold-stratified treatment group (DS2) was germinated under glasshouse conditions, potted in 0.9-L containers, and grown under glasshouse conditions throughout the winter. A fourth experimental group (DS3) was created from the 20-WAP bulk seed to evaluate the effect of postgermination chilling on seedling growth and development (Table 1). This treatment group consisted of four repetitions of 15 seeds and was cold-stratified identically to group DS2, germinated in a glasshouse, and subjected to a 60-day postgermination chilling period at 4 °C. After postgermination chilling, these plants were grown in a glasshouse for the remainder of winter. In the spring of the first growing season (2016), all plants were moved to an outdoor lath structure for the full season. In the spring of the second growing season (2017), all plants were transplanted to 7.6-L pots using an unaged douglas fir bark substrate (Lane Forest Products, Eugene, OR) amended with 20N-2.6P-10K Multicote 8 (Haifa Chemicals Ltd., Savannah, GA) incorporated at 7 kg/m³ and 5N-0.4P-3.3K Premix Plus (Nursery Connection, Hubbard, OR) incorporated at 10 kg/m³. In the spring of the 2018 growing season, all plants were transplanted to 15.1-L pots using the same substrate and fertilizer. The number of plants that flowered was

Fig. 1. Preliminary observations of lilac seeds and seedlings. (A) Quiescent seedling derived from cold-stratified seed during the first year of growth. (B) Immature extracted seed at the time of sowing. (C) Immature green seed germinating on dampened filter paper in a petri dish from a preliminary trial of direct-sown summer lilac seed.

Table 1. Description of treatment groups for germination and postgermination experiments to evaluate the impact of seed handling post pollination on germination and time to flower of common lilac.

Name ^z	WAP ^y	Seed color ^x	Seed development ^w	Pregermination treatment ^v
GS1	5	Green	Green	None, direct-sown
GS2	10	Yellow-green	Green	None, direct-sown
GS3	15	Green-yellow	Green	None, direct-sown
GS4	20	Yellow	Green	None, direct-sown
DS1	20	Brown	Dry	None, direct-sown
DS2	20	Brown	Dry	Cold stratification, 10 weeks
DS3	20	Brown	Dry	Cold stratification, 10 weeks + 60 d of postgermination chilling

^zAbbreviated name designating treatment group: GS = green seed and DS = dry seed.

^yNumber of weeks after pollination (WAP) when capsules were removed from seed parent, *Syringa vulgaris* 'Ludwig Spaeth'.

^xColor description of seed and capsule at the time of collection.

^wPhase of seed development including immature green seed to physiologically dormant dry seed.

^vMethod of seed handling used before sowing.

Fig. 2. Common lilac seed collection and extraction process for green seed (GS) treatment groups GS1, GS2, GS3, GS4 (A–E) and dry seed (DS) treatment groups DS1, DS2, and DS3 (F). (A) Collection of immature predehiscenced capsules. (B) Surface sterilization in 70% ethanol for 1 min. (C) Rinsed with sterile distilled water. (D) Excision of immature green seed. (E) Storage of green seed in sterile distilled water before sowing. (F) Collection of mature dehiscenced capsules and dry seed.

recorded at the beginning of each season, and the plant height was measured in centimeters from the soil surface to the top of the tallest branch at the end of each season (Fig. 5). With the exception of GS1, which did not germinate, all plants from treatment groups GS2, GS3, GS4, DS1, DS2, and DS3 were spaced in a completely randomized design,

with each treatment group having a different number of replicates due to the proportional germination rate of each treatment.

Statistical analysis. For the germination experiment, observations of six treatment groups, GS1, GS2, GS3, GS4, DS1, and DS2, were performed. Treatment group GS1 did not produce any germinated seedlings and was ex-

cluded from the analysis of variance (ANOVA). Percent germination means were normally distributed and passed Levene's test for homogeneity of variance ($F = 1.57$; $P = 0.23$). Means were separated using Tukey's honestly significant difference test ($\alpha = 0.05$), with a minimum significant difference of 29.7% germination (Fig. 3). Error terms were reported as the SEM.

Fig. 3. Percent germination among *Syringa vulgaris* seed collected at six developmental stages and pregermination treatments: green seed (GS) 1 at 5 weeks after pollination (WAP), GS2 at 10 WAP, GS3 at 15 WAP, GS4 at 20 WAP, dry seed (DS) 1 at 20 WAP, and DS2 at 20 WAP after a 10-week stratification period. Data were subjected to an analysis of variance ($\alpha = 0.05$) and differences were reported according to Tukey's honestly significant difference. Bar colors represent an approximation of the original seed/capsule color of germination treatments.

For the postgermination experiment, observations of six treatment groups, GS2, GS3, GS4, DS1, DS2, and DS3, were performed. Due to low germination rates during the first experiment, treatment group GS2 had a small sample size ($n = 3$) and was excluded from the ANOVA. Mean heights (cm) were normally distributed but failed Levene's test for homogeneity of variance ($F = 9.34$; $P < 0.0001$). After natural log transformation, treatment means [$\ln(\text{mm})$] passed Levene's test ($F = 0.73$; $P = 0.5702$). Least-squares means were reported from log-transformed data and back-transformed [$e^{\ln(\text{mm})}$] to the original scale. Least-squares means were separated using the Tukey-Kramer test ($\alpha = 0.05$) for unequal sample sizes. Error terms were reported from 95% confidence intervals and back-transformed to the original scale.

Results and Discussion

Germination experiment. Significant differences in percent germination ($P < 0.001$) were observed among the treatment groups (Fig. 6). Of the treatments groups that produced viable seedlings (no germination was observed in GS1), GS2 showed the lowest percent germination of 7%, whereas GS3 and GS4 showed higher percent germination of 58% and 80%, respectively; however, they were not significantly different from each other. Intermediate germination of 42% was observed in DS1. This agrees with previous studies of tree lilacs that reported mature, yellow capsules and seed with high moisture content collected during a later WAP period that produced higher germination rates compared with dry seed (West et al., 2014). Treatment groups GS3 and GS4 were not significantly different from the cold-stratified treatment group DS2, which had 62% germination. These results indicated that lilac seed collected while still green at 15 and 20 WAP can produce similar germination rates compared with the traditional method of lilac seed germination, which recommends a minimum of 2 months of cold stratification (Dirr and Heuser, 2006). Early germination of treatment groups GS2, GS3, GS4, and DS1 allowed them to grow into the quiescent state before their first winter. There is limited research related to early sowing of woody plants before desiccation/maturation. In the case of common lilac, prior research found that dormancy was primarily due to mechanical restraint of endosperm rather than physiological dormancy of the embryo (Junttila, 1973a). Chilling and gibberellin treatment increased the growth potential of embryos (Junttila, 1973a). Our research illustrates that sowing before desiccation can apparently avoid resistance of the endosperm to allow early germination without chilling. Germination of American basswood (*Tilia americana*) seed increased during weekly intervals until reaching a maximum of 52%, after which it declined precipitously (Vanstone and Ronald, 1982). Our findings showed a similar trend of an increasing germination percentage to a maximum of 80%

Fig. 4. Winter comparison of (A) foliated dormant lilac seedlings from green seed collected 20 weeks after pollination (WAP) and (B) defoliated dormant seedlings from dry seed collected 20 WAP.

Fig. 5. Common lilac seedlings from treatment groups: green seed (GS) 2 at 10 weeks after pollination (WAP), GS3 at 15 WAP, GS4 at 20 WAP, dry seed (DS) 1 at 20 WAP, and DS2 at 20 WAP after a 10-week stratification period. Seedlings in each seed treatment group represent the average plant height after the first full growing season. Scale bar = 5 cm.

Fig. 6. Germination of common lilac seedlings 1 month after sowing of direct-sown, green seed (GS) and dry seed (DS) treatment groups GS1, GS2, GS3, GS4, and DS1 harvested at 5, 10, 15, 20, and 20 weeks after pollination. Treatments consist of 60 seeds divided into lots of 15.

for the GS4 group, but capsules that had turned brown (DS1) had a greatly reduced germination percentage. Green seeds of Korean mimosa (*Albizia kolkora*) sown before maturation/desiccation, at which time seeds develop a hard seedcoat that prevents germination, germinated quickly and at a high percentage with no pretreatment (scarification). This observation demonstrates the opportunity to successfully direct-sow some hard-seeded species before sclerification of the testa.

Ease of seed extraction varied across treatment groups. Early seed extraction in treatment groups GS1 and GS2 required delicate removal of the capsule from the seed; great

care was taken not to damage the immature, green seed (Fig. 2D). Seeds were easily damaged if touched with forceps and were tightly held in the locules. Seed extraction became easier as treatment groups progressed in WAP, with GS3 and GS4 requiring less invasive cutting of the capsule. For GS3 and GS4, seeds were removed by lightly scoring the capsule sutures with a scalpel, piercing the proximal end of the capsule with the scalpel tip, and twisting the scalpel until the capsule opened. Seeds were less tightly held in the locules and would often fall out after opening the capsules. The easiest seed extraction was from dry, dehiscent capsules of treatment groups DS1

and DS2. Dried seeds could be handled without damage (Fig. 2F).

Postgermination experiment. Winter observations of the direct-sown treatment groups GS2, GS3, GS4, and DS1 revealed that all plants retained their foliage during their first winter dormancy, except for plants from DS1 (Fig. 4). All plants from treatment groups GS2, GS3, and GS4 survived, and only one plant from the defoliated DS1 group died. Mortality was relatively high in the DS3 treatment group, which was subjected to 60-d postgermination chilling after cold stratification and germination. Seven of the 30 (23%) treated plants died.

Differences in seedling height were observed in the first season; however, seedlings from all treatment groups were of similar height in the second and third growing seasons (Fig. 7). In the first season, seedling heights of treatment groups GS3 (13.5 ± 0.6 cm) and GS4 (15.6 ± 0.5 cm) were greater than those of dry seed groups DS1, DS2, and DS3, with heights of 3.6 ± 0.7 , 3.7 ± 0.6 , and 4.5 ± 0.7 cm, respectively ($P > 0.0001$). Because GS4 and DS1 were both collected and sown at 20 WAP, this difference in seedling height was most likely due to increased vigor in the GS4 group. However, seedlings in the GS3 group were collected and sown at 15 WAP; these differences could have resulted from the seedlings having an additional 5 weeks to grow, greater vigor, or a combination thereof. In the first season, the tallest plants were in treatment group GS2; however, low germination yielded only three plants for evaluation, and GS2 was excluded from statistical comparisons.

Flower development. At the beginning of the third growing season, two plants in the GS3 treatment and one plant in the GS4 treatment produced flowers, which was insufficient for statistical analyses. However, in the beginning of the fourth season, 88 of the total 175 plants in the trial flowered. No differences were found in the percentage of plants that flowered among treatments or replicates ($P = 0.1983$) (Fig. 8). Treatment group GS2 had 100% flowering in the fourth season. However, because of low germination yielding only three individuals in the treatment, GS2 was excluded from analyses. Previous work involving tree lilacs (West et al., 2014) using green seed sowing did not report time to flower; therefore, it is unclear if these results are consistent across species or even cultivars. During Spring 2020, several individuals flowered from open-pollinated seed collected in 2018 from a 'Tiny Dancer' $\times$ 'Old Glory' hybrid (Contreras and Hoskins, personal observation), which is far more precocious than flowering reported from the cross-combination that was the focus of this study. This suggests that breeders seeking early flowering in common lilac are more likely to achieve that using genetic methods (parent selection) than the cultural methods we explored.

Conclusions

The germination experiment in 2015 revealed that differences in germination depend on when the seed was collected. In

Fig. 7. Seedling height after one, two, and three growing seasons of *Syringa vulgaris* seed collected at six developmental stages and pregermination treatments: green seed (GS) 3 at 15 weeks after pollination (WAP), GS4 at 20 WAP, dry seed (DS) 1 at 20 WAP, DS2 at 20 WAP after a 10-week stratification period, and DS3 at 20 WAP plus stratification and 60 d of postgermination chilling. Data were subject to an analysis of variance ($\alpha = 0.05$) and differences are reported according to Tukey's honestly significant difference.

Fig. 8. Percent of *Syringa vulgaris* seedlings that flowered at the beginning of the fourth growing season according to the developmental stage of the seed at the time of collection: green seed (GS) 3 at 15 weeks after pollination (WAP), GS4 at 20 WAP, dry seed (DS) 1 at 20 WAP, DS2 at 20 WAP plus a 10-week stratification period, and DS3 at 20 WAP plus stratification and 60 d of postgermination chilling. Data were subject to an analysis of variance ($\alpha = 0.05$), although no differences were found. Bar colors represent an approximation of the original seed/capsule color of germination treatments.

summer, as capsules and seeds fade from green to yellow at 15 to 20 WAP, mature seeds with high moisture content can be extracted and sown directly to achieve germination comparable to that of traditional methods without the need to expose the seeds to months of cold stratification. The resulting seedlings from these GS treatments also grew into the first-year quiescent phase, producing

several sets of leaves and an extensive root system earlier than seedlings grown from traditional methods. The increased size of the seedlings observed in treatments GS3 and GS4 in the first growing season was short-lived, but it could allow early selection based on obvious vegetative traits such as leaf color. Additionally, increased vegetative growth during the first year would provide

more material from which to collect DNA samples for researchers or breeders using molecular methods. When seedlings were measured in the two subsequent growing seasons, the smaller seedlings in the DS treatments had caught up, suggesting that there is no sustained benefit to breeders with regard to producing larger plants by using a green seed method. Similarly, there was not a clear benefit of reducing the time to flower and, consequently, accelerating the timeline for breeders by using green seed methods.

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