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Assessment of Controlled Crossing Success Without Pollinator Exclusion in Pawpaw [*Asimina triloba* (L.) Dunal] Cultivars

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Abstract

The North American pawpaw [*Asimina triloba* (L.) Dunal] is the largest edible tree fruit native to the United States and is being grown in orchards by small growers in Kentucky. There are currently few university-based pawpaw breeding programs, with most ongoing breeding conducted by private breeders and hobbyists. Pawpaw flowers bloom in early spring and are pollinated by flies, beetles, and ants. Controlled pollination methods vary widely, with some breeders bagging flowers before and after hand pollination to exclude pollinators, and others leaving flowers unprotected. Even when flowers are bagged, pollination may still occur if small insects, such as ants, enter bags and pollinate pawpaw flowers. Since pawpaw pollinators are lethargic in cool spring temperatures at flowering, many private breeders and enthusiasts do not attempt to exclude pollinators during controlled crosses, leading to questions of parentage. The objective of this study was to examine the efficacy of controlled spring pawpaw crosses performed without bagging flowers before or after hand pollination and to verify parentage using simple sequence repeat (SSR) markers. Crosses were made over two years between the flowers of the pawpaw cultivars 'Sunflower' and 'Susquehanna', as well as selfs, without bagging prior to or after crossing. Seeds were collected from resulting fruit and the seedlings grown out in a greenhouse and then were planted in an orchard. DNA was extracted from young leaves of parents and offspring. PCR was performed using Simple Sequence Repeat markers, for the loci Pp-B3, Pp-B103, Pp-G124, Pp-B129, and Pp-G119. PCR products were separated by capillary electrophoresis for genotypic fingerprinting. For the cross 'Sunflower' × 'Susquehanna', 77.4% of the seedlings were of the expected progeny, and for 'Susquehanna' × 'Sunflower', 65.4% of the seedlings were of the expected progeny. Selfs of 'Sunflower' × 'Sunflower' and 'Susquehanna' × 'Susquehanna' did not yield progeny, confirming that pawpaw usually requires out-crossing. Although high levels of (72%) of crossing success can be achieved without bagging protection before and after hand pollination of flowers, a high percentage of crosses will still be of unexpected parentage, suggesting pollinator exclusion is helpful.

Introduction

The North American pawpaw [*Asimina triloba* (L.) Dunal] is the largest edible tree fruit native to the United States and is being commercially produced on a small scale as a niche fruit crop in the Midwestern and southeastern U.S. (Darrow 1975). Pawpaw fruit has fresh-market appeal for farmers' markets, community-supported agriculture, and organic markets, as well as processing potential for frozen pulp production and value-added products (Archbold et al. 2003; Crabtree et al. 2014; Duffrin and Pomper 2006; Pomper and Layne 2004; Templeton et al. 2003). The ripe fruit has a soft, creamy, yellow-orange flesh and is rich in antioxidants, vitamins, minerals, amino acids, and essential fatty acids (Brannan et al. 2021; Kobayashi et al. 2008;

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Nam et al. 2019; Peterson et al. 1982).

Efforts to domesticate the pawpaw began in the early 20th century (Peterson 1991; Zimmerman 1941). In 1916, the American Genetic Association sponsored a contest to identify superior pawpaw selections. The contest generated significant interest, and it was thought that "intelligent breeding" would support the development of a pawpaw industry (Peterson 2003; Pomper and Layne 2004; Popenoe 1916, 1917). During the first half of the twentieth century, numerous superior wild selections were collected and maintained by horticultural enthusiasts and scientists (Peterson 1991, 2003; Zimmerman 1941). Between approximately 1900 and 1960, at least 56 pawpaw clones were selected and named. However, many of these selections were eventually lost because of neglect, abandonment of collections, and inadequate recordkeeping (Peterson 1991). More than 50 pawpaw cultivars are now commercially available, many of which originated as superior wild selections or from breeding efforts conducted by private enthusiasts (Peterson 2003; Pomper et al. 2008; Pomper and Layne 2004). The Kentucky State University (KSU) Pawpaw Breeding Program has made important contributions to cultivar development and has released five cultivars: 'KSU-Atwood™' in 2009, 'KSU-Benson™' in 2016, 'KSU-Chappell™' in 2018, and 'KSU-Dunnigan™' and 'KSU-Pomper's Choice™' in 2025 (Pomper et al. 2020).

Pollination and fruit set have been a concern to growers of pawpaw and plants related to pawpaw. Low fruit set in pawpaw relatives such as custard apple (*Annona squamosa* L.) and cherimoya (*Annona cherimola*) is often due to poor pollination which has been attributed to both the external and internal factors, such as very high and low humidity prevailing at the time of flowering, soil moisture stress, competition between vegetative and floral growth, hypogyny, protogynous dichogamy, poor pollen germination and lack of insect pollinators (Richardson and Anderson 1996).

Pawpaw is a diploid species ($2n = 2x = 18$) with dark maroon flowers that are strongly protogynous (Willson and Schemske 1980). In spring, flowers emerge before leaves, with bloom typically occurring in April in Kentucky (Pomper and Layne 2004) (Fig 1). Flowers are pollinated primarily by flies, beetles, and ants, which can be relatively lethargic pollinators under the cool temperatures that often prevail during flowering (Thapa Magar et al. 2026). Pawpaw is generally considered to be self-incompatible or highly self-unfruitful (Layne 1996; Pomper and Layne 2004; Thapa Magar et al. 2025). Using simple sequence repeat (SSR) markers, Thapa Magar et al. (2025) demonstrated that the cultivar 'Sunflower' exhibited a low rate of self-fertilization following hand self-pollination, with selfing rates of 7.1% in 2016 and 4.7% in 2017.

Since only a few university-based breeding programs currently exist, much of the ongoing pawpaw breeding is conducted by private breeders and hobbyists. Controlled pollination methods vary widely. Some breeders bag flowers before and after hand pollination to prevent additional insect pollination and contamination of crosses by foreign pollen, whereas others leave flowers unprotected. Even when flowers are bagged, insect pollination may still occur if small insects, such as ants, enter the bags and transfer pollen to receptive flowers (Thapa Magar et al. 2026). In addition, pawpaw flowers are delicate and can be damaged during repeated handling associated with bagging and unbagging (Pomper, personal communication). As a result, many private breeders do not use pollinator exclusion during controlled crosses. Additionally, the thorough coverage of the stigmatic surface with pollen via hand pollination and the cool spring weather slowing the pollinator activity has been used as justification by many private breeders and enthusiasts in breeding without bagging flowers for pollinator exclusion.

Given the increasing number of cultivars released by enthusiasts and private breeders, and the importance of accurate pedigree information for breeding and cultivar development, it is important to determine whether controlled crosses in cool spring conditions conducted without pollinator exclusion produce progeny of the intended parentage. Therefore, the objective of this study was to evaluate the efficacy of controlled pawpaw crosses performed without bagging flowers before or after hand pollination and to verify parentage using

simple sequence repeat (SSR) markers.

Materials and Methods

Plant Material. Crosses and selfs were made in 2016 and 2017 with the pawpaw cultivars 'Sunflower' and 'Susquehanna' as described by Thapa Magar et al. (2025) at the KSU Harold R. Benson Research and Demonstration Farm in Frankfort, Kentucky. The trees were planted with a spacing of 8 feet between trees and 15 feet between rows in May 2004 at the KSU Harold R. Benson Research and Demonstration Farm in Frankfort, Kentucky (Pomper et al. 2021). In April 2016 and 2017, open maroon flowers on branches were hand-pollinated using cotton-tipped applicators or Q-Tips (Unilever, Englewood Cliffs, NJ). In 2016, for each variety, 250 flowers were self-pollinated, and 250 flowers were cross-pollinated resulting in a total of 1000 pollination events. In 2017, hand-pollination treatments were repeated on two trees of each cultivar, with 50 flowers per treatment, resulting in 200 pollination events. Each year the fruit were harvested at physiological maturity. Seed was collected from the fruit of these crosses and self-pollinations and stratified before planting (Geneve et al. 2003).

DNA Extraction and PCR. In 2025, young leaves from parent and seedling trees of crosses and selfs were extracted and used for PCR DNA fingerprinting. Leaf samples were collected from the parents 'Sunflower' and 'Susquehanna', seedling trees of 'Sunflower' × 'Susquehanna' (62 trees), 'Susquehanna' × 'Sunflower' (52 trees), 'Sunflower' × 'Sunflower' (26 trees), and 'Susquehanna' × 'Susquehanna' (32 trees) and were stored at -15 ºC until DNA extraction. DNA extraction from leaves of parents and seedlings was carried out following the protocol described by Pomper et al. (2010). Polymerase chain reaction (PCR) conditions were performed as outlined by Lu et al. (2011); however, plates were evaluated with a SeqStudio genetic analyzer (Applied Biosystems, Foster City, CA, USA). Five specific pawpaw primer pairs, previously developed and validated, were used to compare genotypes (Lu et al. 2011; Pomper et al. 2010). The primers used were Pp-B3, Pp-B103, Pp-G124, Pp-B129, and Pp-G119 (Table 1). The individuals were genotyped or DNA fingerprinted with GeneMapper Software Version 6.0 (Applied Biosystems, Foster City, CA, USA).

Offspring were classified based on allele sizes across the five loci (Table 2). Individuals with all alleles matching a single parent across all loci were identified as self-pollinated offspring. Offspring exhibiting alleles from both parents across all loci were designated as cross-pollinated. Those containing unknown alleles were labeled as unknown cross-pollinated offspring. The percentage of self- and cross-pollinated offspring was calculated for further analysis.



Figure 1. (A) Pawpaw flower about to shed pollen; (B) Hand-pollination using cotton-tipped applicators or Q-Tips; (C) Lady Beetle pollinating a pawpaw flower with pollen adhering to the body.

Table 1. Simple Sequence Repeat (SSR) primer sequences, fluorescent labels, and simple sequence repeat motifs of five primers developed for pawpaw.

Locus	Primer sequence	Label	Enriched motif	Alleles	Allele Size (bp)
Pp-B3	Forward: GCGAAAACGAACATACCTC	FAM[z]	GA	10[y]	175-197
	Reverse: CCTCCTCCACCACCACTAC				
Pp-B103	Forward: ATGCCCCAACAGAGACTTC	FAM	GA	22	181-341
	Reverse: GGATGAGACACTCGGCTTAC				
Pp-B129	Forward: ACACCAGCCATGATTATGATTC	HEX	GA	13	158-193
	Reverse: TCCTTCTCACTCCATCAACAAC				
Pp-G119	Forward: AAACCGTAGTAAAACCAGACAA	FAM	ATT	7	144-176
	Reverse: GGATAGGAAAACATGGTGATTA				
Pp-G124	Forward: GTAGCCAGGAGGAGATGAACT	HEX	AAT	8	192-209
	Reverse: GGTGATTGGATTGCCTAAAAT				

[z]FAM = 6- Carboxyfluorescein and HEX = Hexachlorofluorescein.
[y]Observed number of alleles and allele size in base pairs (bp) in 24 pawpaw cultivars (Lu et al. 2011)

Table 2. The expected allelic combinations for pawpaw simple sequence repeat (SSR) loci that would amplify, with corresponding allele sizes in base pairs (bp), for the pawpaw parents and crosses.

Genotypes	**Pp-B3**	**Pp-B103**	**Pp-G124**	**Pp-B129**	**Pp-G119**
'Susquehanna'	183/191	264/304	192/204	170/172	158/170
'Sunflower'	187	274/341	197/201	162/179	164
'Sunflower' x 'Susquehanna'	187/183 or 187/191	274/264, 274/304, 341/264, or 341/304	197/192. 197/204, 201/192, or 201/204	162/170, 162/172, 179/170, or 179/172	164/158, or 164/170
'Susquehanna' x 'Sunflower'	183/187 or 191/187	264/274, 264/341 304//274, or 304/341	192/197, 192/197, 204/197, or 204/201	170/162, 170/179, 172/162, or 172/179	158/164 or 170/164
'Sunflower' x 'Sunflower'	187/187	274/341 or 341/274	197/ 201 or 201/197	162/162, 162/179, or 179/179	164/164
'Susquehanna' x 'Susquehanna'	183/191 or 191/183	264/304 or 304/264	192/204 or 204/192	170/172 or 172/170	158/170 or 170/158

Results and Discussion

Cool spring temperatures are often observed during pawpaw flowering. In April 2016, the average high temperature was 67.8 °F, the average low temperature was 44.6 °F, and the mean temperature was 56.2 °F at the KSU Farm (Kentucky Mesonet, Western Kentucky University, kymesonet.org). In April 2017, the average high temperature was 71.5 °F, the average low temperature was 50.9 °F, and the mean temperature was 61.2 °F.

Seedlings from crosses in April of 2016 and 2017 were pooled together and were evaluated using SSR DNA fingerprinting to confirm the parentage of crosses between pawpaw cultivars (Table 3). Among the various cross combinations, 'Sunflower' × 'Susquehanna' seedlings yielded the highest proportion of expected progeny, with 77.4% (48 out of 62) of individuals conforming to the intended parentage. In the reciprocal cross, seedlings of 'Susquehanna' × 'Sunflower' had a lower success rate of 65.4% (34 out of 52) for expected progeny. The self-crosses of 'Sunflower' × 'Sunflower' and 'Susquehanna' × 'Susquehanna' did not yield any self progeny, with all 26 and 32 seedlings, respectively, falling into the unexpected category. The unexpected crosses did not have allele sizes that matched those expected from the intended cultivar crosses or self-pollinations, but were instead similar to allele sizes reported for other pawpaw cultivars (Lu et al. 2011), indicating that the progeny resulted from contaminating pollen introduced through open pollination following the manual pollinations.

In this study, we assessed the success rate of achieving desired crosses via hand-pollination of flowers under cool spring conditions without bagging before and after pollination, using molecular markers to verify the breeding method. SSR marker inheritance indicated that overall, almost 72% of crosses were the intended cross. In pawpaw, protogynous flowering and insect-mediated pollination facilitate cross-fertilization. Pollen from the male stage flower must be transferred to the female stage flower of a different genotype for successful fruit set in pawpaw. Thapa Magar et al. (2026) identified five orders of insects observed during the bloom cycle of pawpaw cultivars: Diptera, Coleoptera, Hymenoptera, Hemiptera, and Lepidoptera, with Diptera and Coleoptera as the primary insect orders observed and likely pollinators. No honeybees were present, confirming that bees are not pollinators of pawpaw. Willson and Schemske (1980) also suggested that Drosophila, other flies, and beetles pollinate pawpaw based on general floral visitation, The pawpaw flowers' yeasty, fermenting fruit-like scent likely attracted flies and beetles and the use of lures in pawpaw orchards to attract Diptera and Coleoptera could improve fruit set and crop yield (Goodrich et al. 2023). Manual pollination using a paintbrush or applicator ensures thorough coverage of stigmatic surfaces and has been suggested to reduce the likelihood of contamination from non-target pollen sources. Since pawpaws are pollinated by lethar-

Table 3. Classification of pawpaw progeny as a result of crossing in April 2016 and 2017 into expected and unexpected parentage groups based on SSR marker fingerprint.

Genotypes	Expected Cross or Self		Unexpected Cross[z]		
	Number of cross or self	Percentage	Number of cross	Percentage	**Total (n)**
'Sunflower' × 'Susquehanna'	48	77.4	14	22.6	**62**
'Susquehanna' × 'Sunflower'	34	65.4	18	34.6	**52**
'Sunflower' × 'Sunflower'	0	0	26	100	**26**
'Susquehanna' × 'Susquehanna'	0	0	32	100	**32**

[z]Observed allele sizes did not match those expected from the intended cultivar crosses or self-pollinations but were instead similar to allele sizes reported for other pawpaw cultivars (Lu et al. 2011), indicating that the progeny resulted from contaminating pollen introduced through open pollination following the manual pollinations.

gic insects such as flies, breeders commonly do not bag flowers before and after pollination to protect them from pollination by insects carrying foreign pollen. It is likely that these insects are more lethargic than honeybees in the cooler spring months when pawpaw flowers are in bloom, and therefore, these insects do not bring genetically different pollen to pawpaw flowers at a high level. The thorough coverage of the stigmatic surface with pollen via hand pollination and the cool spring weather slowing the pollinator activity has been used as justification by many private breeders and enthusiasts in breeding without pollinator exclusion. High levels (72%) of crossing success can be achieved without bagging protection before and after hand pollination of flowers; however, a high percentage of crosses are still of unexpected parentage, which is undesirable.

Pawpaw has generally been considered to be self-incompatible or highly self-unfruitful (Pomper and Layne 2004; Thapa Magar et al. 2025). Pawpaw is characterized by protogynous flowering and complex reproductive behavior (Losada et al. 2017; Pomper and Layne 2004). This current study further supports this observation in that the self-cross of 'Sunflower'× 'Sunflower' did not produce any offspring that were the result of selfing. Similarly, the combination 'Susquehanna' × 'Susquehanna' also did not yield any selfed progeny, with all 32 individuals (100%) falling into the unexpected category. Although the work of Thapa Magar et al. (2025) showed that 'Sunflower' exhibited self-pollination and some self-compatibility, we did not observe any evidence of selfing in 'Sunflower' and 'Susquehanna'.

Conclusion

In conclusion, hand pollination of pawpaw flowers in cool spring conditions without bagging, before and after pollination, can result in a high level of desired crossing. However, bagging protection before and after hand pollination of flowers in cool spring conditions to exclude pollinators is important in crossing strategies to avoid unexpected parentage. Although high levels of (72%) of crossing success can be achieved without bagging protection before and after hand pollination of flowers, a high percentage of crosses will still be of unexpected parentage, suggesting pollinator exclusion is helpful.

Acknowledgments

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