# The North American Pawpaw: Botany and Horticulture

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#### I. INTRODUCTION

The North American pawpaw [Asimina triloba (L.) Dunal] grows wild in mesic hardwood forests of 26 states in the eastern United States, flourishing in deep, fertile soils of river-bottom lands where it grows as an understory tree or thicket-shrub (Kral 1960; Callaway 1990; Callaway 1993). Pawpaws can be grown successfully in USDA plant hardiness zones 5 (minimum of –29°C) through 8 (minimum of –7°C) (Kral 1960). This tree produces the largest edible fruit native to the United States; it may reach up to 1 kg in size (Darrow 1975). The pawpaw fruit has both fresh market and processing potential, with an intense flavor that resembles a combination of banana, mango, and pineapple. Natural compounds in the leaf, bark, and twig tissues of pawpaw possess insecticidal and anti-cancer properties (McLaughlin 1997). The unique qualities of the fruit, ornamental value of the tree, and the potential for useful bioactive compounds suggest that pawpaw has great potential as a new high-value crop.

Although pawpaw has great potential for commercial production, orchard plantings remain limited. Currently, most pawpaw fruit for sale are collected from wild stands in the forest. However, in a number of states, including Alabama, California, Kentucky, Maryland, Michigan, Missouri, North Carolina, Ohio, and West Virginia, in the United States, small private orchards, usually less than 1 ha in size, have been planted and will be coming into production soon. There are also pawpaw plantings in Italy (Bellini et al. 2003), China, Israel, Japan, Romania, Belgium, and Portugal. In the United States, pawpaw fruit and products are mainly sold at farmer's markets, directly to restaurants, and via entrepreneurs on the Internet. Pawpaw fruit were sold in 2003 at the Farmer's Market in Lexington, Kentucky, for \$6.50 per kg. Local delicacies made from the fruit include pawpaw ice cream, compote, jam, and wine. However, at present the grower base is insufficient to establish a commercial processing industry.

Nursery wholesale and retail tree production represent an added economic opportunity for entrepreneurs beyond that of orchard production. Pawpaw trees currently sell for higher prices than most other fruit trees since they are attractive to homeowners in ornamental plantings, edible landscapes, specialty gardens, and habitat restoration (Layne 1996). In addition, *Asimina* spp. are suitable for butterfly gardens, as they attract the zebra swallowtail (*Eurytides marcellus* Cramer), for whom they are the exclusive larval host plant (Damman 1986; Haribal and Feeny 1998).

Many challenges are encountered in developing production practices for a new crop. Cultural practices can affect important aspects of plant growth and influence the overall dynamics of the production system.

The objective of this chapter is to review the botany and horticulture of the pawpaw and to summarize recent research efforts that have been conducted in an attempt to develop production recommendations for this promising new crop.

### II. HISTORY

Pawpaws have a well-established place in folklore and American history. "Where, oh where, is dear little Nellie (Sallie, etc.)? 'Way down vonder in the pawpaw patch." This traditional American folk song and dance was quite popular once and fall hunting for pawpaws in the woods is a cherished tradition for many rural families in the southeastern United States. The first report of pawpaw dates back to 1541 when followers of the Spanish explorer Hernando de Soto found Native Americans growing and eating pawpaws in the valley of the Mississippi (Pickering 1879). The Native Americans used the bark of pawpaw trees to make fishing nets. John Lawson (1709) in A New Voyage to Carolina referred to pawpaws "as sweet, as any thing can well be. They make rare Puddings of this Fruit." John Filson (1784), an early settler, promoter and developer of Kentucky, stated that "the pappa-tree does not grow to a great size, is a soft wood, bears a fine fruit much like a cucumber in shape and size, and tastes sweet." Daniel Boone and Mark Twain were reported to have been pawpaw fans. Lewis and Clark recorded in their journal (18 September 1806) how pawpaws helped save them from starvation. "Our party entirely out of provisions subsisting on poppaws. We divided the buiskit which amounted to nearly one buiskit per man, this in addition to the poppaws is to last us down to the Settlement's which is 150 miles. The party appear perfectly contented and tell us that they can live very well on poppaws." John James Audubon painted the yellow-billed cuckoo on a native pawpaw tree (ca. 1827). On 9 August 1882, three sons of Randolph McCoy (clan leader) were tied to pawpaw bushes and executed by the rival Hatfield family during the famous Hatfield-McCoy feud along the Kentucky-West Virginia border (Owens 1994). Several American towns, townships, creeks and rivers were named after the pawpaw during the 19th century.

Interest in pawpaw as a fruit crop was evident in the early 1900s (Little 1905; Popenoe 1916, 1917; Zimmerman 1938, 1941; Thomson 1974; Peterson 1991). At about this same time, interest in another native fruit, the blueberry (*Vaccinium* sp.), was also increasing. One reason for the failure of pawpaw to become as popular as blueberry was likely related to the rapid perishability of the fruit (Popenoe 1916, 1917). However, interest in pawpaw grew in the years between 1950 and 1985, nurtured

by the enthusiasm of individuals in the Northern Nut Growers Association (NNGA) (Peterson 2003). Since 1985, various associations and institutions committed to pawpaw development have emerged. The PawPaw Foundation (PPF) was founded in 1988, by R. Neal Peterson. as a nonprofit organization dedicated to the research and development of the pawpaw as a new fruit crop for farmers and consumers. In 1990. a full-time pawpaw research program was initiated at Kentucky State University (KSU) by Brett Callaway (Callaway 1992) and was expanded by Desmond Layne from 1993 to 1997 (Layne 1996) and has been under the direction of Kirk Pomper since 1998 (Pomper et al. 1999). For over 10 years at KSU there have been cooperative research projects with PPF to advance our understanding of the pawpaw. Two international pawpaw conferences have been held. The first conference was held in 1994 at the Western Maryland Research and Education Center in Keedysville, Maryland, where about 45 scientists, nurserymen, entrepreneurs, and enthusiasts attended. The second conference was held at KSU in Frankfort, Kentucky and had over 130 people in attendance (Pomper et al. 2003a). The Ohio Pawpaw Growers Association (Albany, Ohio) was established in 2000 to organize and advance the development of a pawpaw industry in Ohio. The Ohio Pawpaw Growers Association, PPF, and the KSU pawpaw program, as well as other associations and institutional programs that will likely be established, will be important in promoting, marketing and consumer education programs concerning pawpaw.

## III. BOTANY

## A. Taxonomy

The tropical custard apple family, Annonaceae, is the largest primitive family of flowering plants, containing approximately 130 genera and 2300 species (Conquist 1981). This family includes several delicious tropical fruits such as the custard apple (Annona reticulata L.), cherimoya (A. cherimola Mill.), sweetsop or sugar apple (A. squamosa L.), atemoya (A. squamosa × A. cherimola), and soursop (A. muricata L.) (Bailey 1960). The genus Asimina is the only temperate-zone representative of the tropical Annonaceae, and includes nine species, most of which are native to the extreme southeastern regions of Florida and Georgia (Kral 1960; Callaway 1990, 1993). These species include Asimina incarna (Bartr.) Exell. (flag pawpaw), A. longifolia Kral, A. obovata (Willd.) Nash, A. parviflora (Michx.) Dunal (dwarf pawpaw), A. pygmaea (Bartr.) Dunal, A. reticulata Shuttlw. ex Chapman, A. tetramera Small (opossum pawpaw), A. × nashii Kral and A. triloba (Kral 1960). All

Asimina species are diploids, 2n = 2x = 18, with the possible exception of *A. pygmaea* (Bartr.) Dunal, for which chromosome counts have not been reported (Bowden 1948; Kral 1960). Triploid *A. triloba* hybrids have also been reported to exist (Bowden 1949).

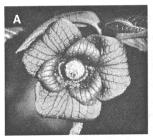
The genera of Annonaceae have been difficult to separate; therefore, the pawpaw has undergone a number of nomenclature changes (Kral 1960). Linnaeus first classified it as *Annona triloba* in 1753. Ten years later, Adanson assigned the pawpaw to the *Asimina* genus. It remained in this classification for several years, until 1803 when Michaux reclassified pawpaw as *Orchidocarpum arietinum*. Four years later Persoon reclassified it as *Porcelia triloba*. In 1817 Dunal returned pawpaw to *Asimina*, but Torrey and Gray transferred it to the genus Uvaria in 1838. In 1886, Gray reconsidered the classification and returned pawpaw to *Asimina*. *Asimina triloba* (L.) Dunal is the nomenclature currently accepted (Kral 1960).

The large-fruited pawpaw, *Asimina triloba*, is likely the best-known member of the *Asimina* genus. This species has the most northerly and largest native range of the genus, extending from northern Florida to southern Ontario, Canada, and as far west as eastern Nebraska and Texas (Kral 1960; Callaway 1990, 1993). The fruit of *A. triloba* has the greatest commercial potential of the *Asimina* genus due to the large size and usually pleasing flavor.

## B. Morphology and Anatomy

Pawpaw is a moderately small, deciduous tree or shrub that flourishes in the deep, rich fertile soils of river-bottom lands of the forest understory (Kral 1960). Trees may attain 5 to 10 m in height and are usually found in patches, due to root suckering (Kral 1960; Layne 1996). In sunny locations, trees typically assume a pyramidal habit, with a straight trunk and lush, dark-green, long, drooping leaves. Leaves occur alternately, are obovate-oblong in shape, glabrous, with a cuneate base, acute midrib, and may be 15 to 30 cm long and 10 to 15 cm wide. Vegetative and flower buds occur at different nodes on the stem, the flower buds being basipetal. Vegetative buds are narrow and pointed, and the flower buds are round and covered with a dark-brown pubescence.

The dark maroon-colored flowers of the pawpaw are hypogynous and strongly protogynous (Willson and Schemske 1980). Flowers are pendant on nodding, with sturdy pubescent peduncles up to 4 cm long (Kral 1960). The mature flowers have an outer and inner whorl of three, maroon-colored, three-lobed petals (Fig. 7.1). The inner petals are smaller and fleshier, with a nectary band at the base. The flower has a fetid aroma. Flowers have a globular androecium and a gynoecium usually







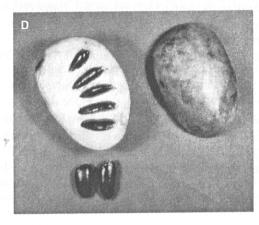




Fig. 7.1. (A) Mature flower with an outer and inner whorl of three maroon-colored, three-lobed petals. (B) A mature pawpaw flower and developing cluster from an earlier flower. (C) Pawpaw cluster with ripe fruit. (D) A fruit cut open lengthwise and seeds removed. (E) A pawpaw tree showing pyramidal growth habit in full sun.

composed of three to seven carpels resulting in three to seven fruited clusters (Kral 1960); up to nine-fruited clusters have been noted (Fig 7.1). Flowers emerge before leaves in spring (about April in Kentucky). Pawpaw blossoms occur singly on the previous year's wood, reaching up to 5 cm in diameter.

Pawpaw's custard-like fruits are berries (Dirr 1990). The fruit have an oblong shape, green skin, a pleasant but strong aroma when ripe, and intense flavor (Peterson 1991; Shiota 1991; Layne 1996). However, flavor varies among cultivars, with some fruit displaying complex flavor profiles. Fruit from poor-quality pawpaw genotypes can have a mushy texture, lack sweetness, and have an overly rich flavor with turpentine or bittersweet aftertaste; many wild pawpaws have poor eating quality. Fruit from superior genotypes have a firm texture, a delicate blend of flavors, are rich but not cloying, and have no bitter aftertaste. The flavor of a pawpaw fruit can intensify when it over-ripens, as with banana, result-

ing in pulp that is excellent for use in cooking. The fruit are oblong-cylindrical, typically 3 to 15 cm long, 3 to 10 cm wide and weigh from 100 to 1000 g. They may be borne singly or in clusters that resemble the "hands" of a banana plant. In the fruit, there are two rows of seeds (12 to 20 seeds) that are brown and bean shaped and that may be up to 3 cm long. The seed and skin of the fruit are generally not eaten. The endosperm of the seeds contains alkaloids that are emetic (Vines 1960) and if chewed may impair mammalian digestion. Pawpaw fruit allergies have been reported in some people (Barber 1905). Seed lipid profiles include octanoate and positional monoene fatty acid isomers (Wood and Peterson 1999). In the wild, the primary consumers and seed dispersers are raccoons [Procyon lotor (L.) Elliot], red foxes [Vulpes fulvus (Desmarest) Merriam], and opossums (Didelphis virginiana kerr) that eat fruit that has fallen to the ground. Deer (Odocoileus virginianus) will also eat whole pawpaw fruit when it is available and they may also disperse seed.

The pawpaw fruit has a high nutritional value (Table 7.1) (Peterson et al. 1982; Jones and Layne 1997). Pawpaw and banana are similar in dietary fiber content and overall nutritive composition. Pawpaw has three times as much vitamin C as apple, twice as much as banana, and one third as much as orange. Pawpaw has six times as much riboflavin as apple, and twice as much as orange. Niacin content of pawpaw is twice as high as banana, 14 times higher than apple, and four times higher than orange. Pawpaw and banana are both high in potassium, having about twice as much as orange and three times as much as apple. Pawpaw has one and a half times as much calcium as orange, and about 10 times as much as banana or apple. Pawpaw has two to seven times as much phosphorus, four to 20 times as much magnesium, 20 to 70 times as much iron, five to 20 times as much zinc, five to 12 times as much copper, and 16 to 100 times as much manganese, as do banana, apple, or orange. Pawpaw exceeds apple in all of the essential amino acids, and exceeds or equals banana and orange for some. Pawpaw has 32% saturated, 40% monounsaturated, and 28% polyunsaturated fatty acids as compared to banana, which has 52% saturated, 15% monounsaturated, and 34% polyunsaturated fatty acids. Pawpaw is an excellent food source.

#### C. Genetic Resources

Efforts to domesticate the pawpaw began early in the 20th century (Zimmerman 1941; Peterson 1991). In 1916, a contest to find the best pawpaw was sponsored by the American Genetics Association. This contest generated much interest and the sponsors thought that with time and "intelligent breeding" commercial-quality varieties could be developed

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**Table 7.1.** Nutritional comparison of pawpaw with other fruits.<sup>z</sup>

Composition	Units	Pawpaw	Banana	Apple	Orange
Proximal analysis					
Food Energy	cal	80	92	59	47
Protein	g	1.2	1.03	0.19	0.94
Total Fat	g	1.2	0.48	0.36	0.12
Carbohydrate	g	18.8	23.4	15.25	11.75
Dietary Fiber	g	2.6	2.4	2.7	2.4
Vitamins					
Vitamin A	$RE^y$	8.6	8	5	21
Vitamin A	$IU^x$	87	81	53	205
Vitamin C	mg	18.3	9.1	5.7	53.2
Thiamin	mg	0.01	0.045	0.017	0.087
Riboflavin	mg	0.09	0.1	0.014	0.04
Niacin	mg	1.1	0.54	0.077	0.282
Minerals					
Potassium	mg	345	396	115	181
Calcium	mg	63	6	7	40
Phosphorus	mg	47	20	7	14
Magnesium	mg	113	29	5	10
Iron	mg	7	0.31	0.18	0.1
Zinc	mg	0.9	0.16	0.04	0.07
Copper	mg	0.5	0.104	0.041	0.045
Manganese	mg	2.6	0.152	0.045	0.025
Essential amino acids				0	18
Histidine	mg	21	81	3	25
Isoleucine	mg	70	33	8	23
Leucine	mg	81	71	12	47
Lysine	mg	60	48	12	20
Methionine	mg	15	11	2	
Cystine	mg	4	17	3	10 31
Phenylalanine	mg	51	38	5	
Tyrosine	mg	25	24	4	16
Threonine	mg	46	34	7	15
Tryptophan	mg	9	12	2	9
Valine	mg	58	47	9	40

<sup>&</sup>lt;sup>2</sup>Derived from Peterson et al. (1982) and Jones and Layne (1997). Mean value per 100 grams edible portion. Pawpaw analysis was done on pulp with skin, although the skin is not considered edible. Probably much of the dietary fiber, and possibly some of the fat, would be thrown away with the skin.

and an industry begun (Popenoe 1916, 1917; Peterson 2003). However, an industry did not develop. Pawpaw enthusiasts noted that the rapid perishability of pawpaw fruit was the major factor inhibiting commercialization.

Beginning in the 20th century, elite pawpaw selections from the wild were assembled in extensive collections by various enthusiasts and scientists, including Benjamin Buckman (Farmington, Illinois, circa 1900 to 1920), George Zimmerman (Linglestown, Pennsylvania, 1918 to 1941), and Orland White (Blandy Experimental Farm, Boyce, Virginia, 1926 to 1955) (Peterson 1986; Peterson 1991; Peterson 2003; Zimmerman 1941). From about 1900 to 1960, at least 56 clones of pawpaw were selected and named. Fewer than 20 of these selections remain, with many being lost from cultivation through neglect, abandonment of collections, and loss of records necessary for identification (Peterson 1991). Since 1960, additional pawpaw cultivars have been selected from the wild or developed as a result of breeding efforts of hobbyists. More than 40 clones are currently available (Table 7.2) (Jones et al. 1998). The loss of cultivars over the last century may have led to erosion in the genetic base of current

**Table 7.2.** Commercially available pawpaw cultivars.<sup>z</sup>

Cultivar	Description		
Adam's Secret	From Pennsylvania, large fruit, few seeds, skin remains green when ripe.		
Blue Ridge	Selected in Kentucky by Johnny Johnson; has white-fleshed fruit		
Collins	Selected in Georgia.		
Convis	Selected in Goodgan Selected from Corwin Davis orchard. Large fruit size, yellow flesh; ripens 1st week of Oct. in Michigan.		
Davis	Selected from the wild in Michigan by Corwin Davis in 1959.  Introduced in 1961 from Bellevue, Michigan. Medium size fruit, up to 12 cm long; green skin; yellow flesh; large seed; ripens 1st week of Oct. in Michigan; keeps well in cold storage.		
Duckworth A	Low-chill cultivar selected in San Mateo, Florida by Eric Duckworth, seedling of Louisiana native parent; tree with pyramida shape.		
Duckworth B	Low-chill cultivar selected in San Mateo, Florida by Eric Duckworth, seedling of Louisiana native parent; grows no larger than a shrub.		
Estil	Selected by Nettie Estil in Frankfort, Kentucky. Large fruit:		
Ford Amend	Selected from wild seedling of unknown parentage by Ford Amend around 1950. Introduced from Portland, Oregon. Medium-size fruit and earlier than Sunflower; ripens late		
	September in Oregon; greenish-yellow skin; orange flesh.		

(continues)

PRetinol Equivalents—these units are used in National Research Council Recommended Dietary Allowances table (1989).

<sup>\*</sup>International Units.

 Table 7.2.
 Commercially available pawpaw cultivars. z

Cultivar	Description
G-2	Selected from G. A. Zimmerman seed by John W. McKay, College Park, Maryland, in 1942.
Glaser	Colored by P. Claser of Evansville, Indiana, Medium-size Iruit,
IXL	Hybrid of Overleese and Davis; large fruit, yellow flesh; ripens
Jack's Jumbo Kirsten	Selected in California from Corwin Davis seed; large fruit. Hybrid seedling of Taytwo × Overleese; selected by Tom Mansell,
	Aliquippa Penneylyania
LA Native	From LA, blooms late in Tennessee, small fruit, somewhat frost hardy.
Little Rosie	Selected by P. Glaser of Evansville, Indiana. Has small fruit.  Reported to be an excellent pollinator.
Lynn's Favorite	Selected from Corwin Davis orchard. Yellow fleshed, large full,
M-1	Selected from G-2 seed by John W. McKay, College Park,
Mango	Selected from the wild in Tifton, Georgia, by Major C. Collins in 1979. Vigorous growth.
Mary Foos Johnson	Selected from the wild in Kansas by Milo Gibson. Seeding donated to North Willamette Expt. Sta., Aurora, Oregon, by Mary Foos Johnson. Large fruit; yellow skin; butter-color flesh; few goods, ripens first week of Oct. in Michigan.
Mason/WLW	Selected from the wild in Mason, Ohio, by Ernest J. Downing in
Middletown	Selected from the wild in Middletown, Ohio, by Ernest J.  Downing in 1915. Small fruit size.
Mitchell	Selected from the wild in Jefferson Co., Illinois, by Joseph W. Hickman in 1979. Fruit: Medium fruit size, slightly yellow
NC-1	Hybrid seedling of Davis × Overleese; selected by R. Douglas Campbell, Ontario, Canada, in 1976. Large fruit; few seeds; yellow skin and flesh; thin skin; early ripening, 15 Sept. in
	Optopio and early Sent in Kentucky.
Overleese	Selected from the wild in Rushville, Indiana, by W. B. Ward in 1950. Large fruit; few seeds; bears in clusters of three to five;
	ripens 1st week of Oct. in Michigan and early Sept. in Kentucky.
PA-Golden 1	Selected as seedling from seed originating from George Slate collection by John Gordon, Amherst, New York. Early cropping. Medium-size fruit, yellow skin, golden flesh; mature late August in Kentucky and mid-Sept. in New York.
PA-Golden 2	Selected as seedling from seed originating from George State collection by John Gordon, Amherst, New York. Fruit: yellow
PA-Golden 3	Selected as seedling from seed originating from George Slate collection by John Gordon, Amherst, New York. Fruit: yellow skin, golden flesh; matures mid-Sept. in New York.

Cultivar	Description		
PA-Golden 4	Selected as seedling from seed originating from George Slate collection by John Gordon, Amherst, New York. Fruit: yellow		
	skin, golden flesh; matures mid-Sept. in New York.		
Prolific	Selected by Corwin Davis, Bellevue, Michigan, in mid-1980s. Large fruit; yellow flesh; ripens first week of Oct. in Michigan.		
Rebecca's Gold	Selected from Corwin Davis seed, Bellevue, Michigan, by J. M. Riley in 1974. Medium-size fruit; kidney-shaped; yellow flesh.		
Ruby Keenan	Medium-size fruit with excellent flavor.		
SAA-Overleese	Selected from Overleese seed by John Gordon, Amherst, New York, in 1982. Large fruit; rounded shape; green skin; yellow flesh; few seeds; matures in mid-Oct. in New York.		
SAA-Zimmerman	Selected as seedling from seed originating from G. A. Zimmermar collection by John Gordon, Amherst, New York, in 1982. Large fruit; yellow skin and flesh; few seeds.		
Silver Creek	Selected from the wild in Millstedt, Illinois, by K. Schubert. Medium fruit size.		
Sue	Selected in southern Indiana. Medium-size fruit, yellow flesh, skin yellow when ripe.		
Sunflower	Selected from the wild in Chanute, Kansas, by Milo Gibson in 1970. Tree reported to be self-fertile. Large fruit; yellow skin; butter-color flesh; few seeds; ripens early to mid-Sept. in		
	Kentucky and the first week of Oct. in Michigan.		
Sunglo	Yellow skin, yellow flesh, large fruit; fruit ripens 1st week of Oct. in Michigan.		
Sweet Alice	Selected from the wild in West Virginia by Homer Jacobs of the Holden Arboretum, Mentor, Ohio, in 1934.		
Taylor	Selected from the wild in Eaton Rapids, Michigan, by Corwin Davis in 1968. Small fruit; bears up to seven fruit in a cluster; green skin; yellow flesh; ripens 1st week of Oct. in Michigan.		
Taytwo	Selected from the wild in Eaton Rapids, Michigan, by Corwin Davis in 1968. Sometimes spelled Taytoo. Small fruit; light- green skin; yellow flesh; ripens 1st week of Oct. in Michigan.		
Tollgate	Yellow fleshed, large fruit, fruit ripens 1st week of Oct. in Michigan.		
Wells	Selected from the wild in Salem, Indiana, by David Wells in 1990. Small to medium-size fruit; green skin; orange flesh. Ripens mid to late Sept. in Kentucky.		
White	Selected in Kentucky by Johnny Johnson; has white-fleshed fruit.		
Wilson	Selected from the wild on Black Mountain, Harlan Co., Kentucky by John V. Creech in 1985. Small fruit; yellow skin; golden flesh.		
Zimmerman	Selected in New York from G. A. Zimmerman seed by George Slate.		

\*Descriptions derived from Layne (1997), Jones et al. (1998), and unpublished data of K. Pomper. Descriptions come from a wide variety of sources, and most of the cultivars have not been compared for performance side by side at one geographic site.

\*Fruit size categories of small, medium, and large are <100 g, 100 to 150 g, and >150 g,

respectively.

pawpaw cultivars (Huang et al. 1997). Urban encroachment and the resulting destruction of native pawpaw patches may also be leading to a reduction in genetic diversity in the wild.

In 1981, R. Neal Peterson and Harry Swartz began a long-term breeding project that aimed to develop improved pawpaw cultivars (Peterson 1986, 1991, 2003). A collection of about 1500 accessions of openpollinated seedlings was assembled at the University of Maryland Experiment Stations at Queenstown and Keedysville, Maryland. The seed for this germplasm collection was obtained from pawpaw trees that remained at the sites of the historic collections of Buckman, Zimmerman, and the Blandy Experimental Farm, as well as those of Hershey (Downington, Pennsylvania), Allard (Arlington, Virginia), Ray Schlaanstine (West Chester, Pennsylvania), and open-pollinated seed from some modern cultivars.

In 1993, the PPF and KSU embarked on a joint venture to test 10 commercially available pawpaw cultivars and 18 of PPF's advanced selections from the Maryland orchards in a Pawpaw Regional Variety Trial (PRVT) (Layne 1996; Pomper et al. 1999; Pomper et al. 2003d). From 1996 to 1999, 13 universities or private cooperators have established or have attempted to establish PRVT demonstration orchards (Wapello, Iowa; Frankfort and Princeton, Kentucky; Baton Rouge, Louisiana; Keedysville, Maryland; Jackson, Michigan; Lincoln, Nebraska.; Ithaca, New York; Raleigh, North Carolina; Piketon, Ohio; Corvallis, Oregon; West Lafayette, Indiana; and Clemson, South Carolina). Named cultivars that were secured for testing include: 'Middletown' (selected in Ohio), 'Mitchell' (Illinois), 'NC-1' (Ontario, Canada), 'Overleese' (Indiana), 'PA-Golden' (New York), 'Sunflower' (Kansas), 'Taylor' (Michigan), 'Taytwo' (Michigan), 'Wells' (Indiana), and 'Wilson' (Kentucky). The "advanced selections" were chosen based on superior horticultural traits including fruit size and taste, flesh-to-seed ratio, resistance to pests and diseases, and overall productivity on a year-to-year basis. Regional recommendations have not yet been made because more years of performance evaluation are needed.

In 1994, KSU was designated as a satellite repository for *Asimina* preservation in the U.S. Department of Agriculture (USDA), National Plant Germplasm System (NPGS). As a result, germplasm evaluation, preservation, and dissemination are a high priority. The repository orchards currently contain over 1700 accessions collected from the wild in 17 states and more than 40 cultivars. One of the goals of the repository is to assess levels of genetic diversity in native populations, in the repository collection, and in commercially available cultivars. Another goal is to acquire unique germplasm to add to the collection that could be useful in future pawpaw breeding efforts.

## D. Genetic Diversity

A range of molecular markers has been utilized in attempts to evaluate genetic diversity in pawpaw. Rogstad et al. (1991) used a minisatellite probe, M13, to determine the genetic variation in pawpaw collected in five states. Using data from one to 22 samples per population, these authors examined genetic variation at 16 sites both within and among populations. They determined that genetic variation is very low within populations, but moderate genetic variation occurred between populations. They concluded that the low level of genetic variation within populations might be due to clonality of pawpaw patches or inbreeding. However, inbreeding is considered to be rare in pawpaw's reproductive biology, because it is most likely self-incompatible and therefore may require out-crossing (Peterson 1991; Norman et al. 1992).

Huang et al. (1997) used isozymes to evaluate the genetic diversity represented in 32 pawpaw cultivars and advanced selections from the breeding program of R. Neal Peterson of the PPF. These authors determined that the isozyme marker variation in cultivated pawpaw is comparable to those of other long-lived temperate woody perennials of widespread geographic range with insect-pollinated outcrossing breeding systems, secondary asexual reproduction and animal-dispersed seed, thus having a higher level of genetic diversity than Rogstad et al. (1991) had reported (Table 7.3). Huang et al. (1997) acknowledged that the results may have been impacted by non-random selection because several of the trees studied may have been purposely selected by pawpaw enthusiasts for desirable characteristics such as large fruit size or good growth vigor.

Using isozymes, Huang et al. (1998) assessed the level of genetic diversity within wild collected pawpaw accessions at KSU and examined genetic diversity between pawpaw populations from different geographical locations. Isozymes were used to score 23 loci using 25 to 50 trees from each of nine populations. The level of genetic variation found in the KSU repository accessions was similar to that found in cultivated pawpaws (Huang et al. 1997).

Using 12 randomly amplified polymorphic DNA (RAPD) primers, Huang et al. (2000) identified 21 Mendelian markers and determined that the level of genetic diversity in six populations in the KSU repository collection was higher than determined for pawpaw by the same authors using isozymes (Huang et al. 1997, 1998). Huang et al. (2003) have also used additional RAPD markers for fingerprinting pawpaw cultivars. They reported similar levels of genetic diversity in cultivated pawpaw, in terms of Nei's genetic diversity constant (He) and percent polymorphic loci (P), to that reported for wild pawpaw populations by Huang et

**Table 7.3.** Comparison of genetic variation of pawpaw (*Asimina triloba*) with plant species having the same characteristics.

Species characteristics	Polymorphic locus (%) (P) <sup>y</sup>	Expected heterzygosity $(\mathrm{H_e})$
Life form: long-lived woody perennial <sup>z</sup>	64.7 ± 2.7	$0.177 \pm 0.010$
Regional distribution: widespread <sup>z</sup>	$58.9 \pm 3.1$	$0.202 \pm 0.015$
Geographic range: temperate <sup>z</sup>	$48.5 \pm 1.5$	$0.146 \pm 0.000$
Breeding system: outcrossing-animal <sup>z</sup>	$50.1 \pm 2.0$	$0.167 \pm 0.010$
Seed dispersal: animal ingested <sup>z</sup>	$45.7 \pm 3.9$	$0.176 \pm 0.019$
Mode of reproduction: sexual and asexual <sup>z</sup>	$43.8 \pm 3.7$	$0.138 \pm 0.016$
Average of all characteristics <sup>z</sup>	$51.2 \pm 8.2$	$0.168 \pm 0.023$
California cherimoya <sup>x</sup>	73.3	$0.330 \pm 0.064$
California and Spanish cherimoya <sup>w</sup>	44.8	$0.183 \pm 0.044$
Cultivated pawpaw (Isozymes) <sup>v</sup>	44.4	$0.166 \pm 0.048$
Pawpaw wild accessions (Isozymes) <sup>u</sup>	43.5	$0.172 \pm 0.013$
Pawpaw wild accessions (RAPDs) <sup>t</sup>	64	$0.249 \pm 0.022$
Cultivated pawpaw (RAPDs)s		$0.285 \pm 0.160$
Cultivated pawpaw (ISSRs) <sup>r</sup>	80	$0.358 \pm 0.205$

<sup>&</sup>lt;sup>z</sup>Data from Hamrick and Godt, 1989 derived from isozyme studies +/- of standard deviation.

al. (2000). Pomper et al. (2003b) used 10 inter-simple sequence repeat (ISSR) markers, and determined estimates of genetic diversity (P=80% and He=0.358) that were higher than those based on isozymes (P=44% and He=0.172) for cultivated pawpaw, for RAPDs for wild pawpaw accessions (P=64% and He=0.249) and cultivated pawpaw (He=0.285) by Huang et al. (1997, 2000, 2003). These higher diversity values estimated for cultivated pawpaw by the ISSR marker system indicate that this marker methodology has a higher level of discrimination in evaluating genetic diversity in pawpaw than the isozyme or RAPD marker systems and/or that pawpaw has greater levels of genetic diversity than previously found.

#### IV. HORTICULTURE

#### A. Orchard Site Selection

Pawpaw orchards should be located at a site with characteristics that would be well suited for production of other temperate tree fruit species. The planting site should have good air drainage to reduce the risk of damage from late spring frosts that can damage both foliage and flowers. In mid-April in Kentucky, frost damage to flowers and leaves has occurred when early morning temperatures drop to -2.2°C or lower. During the first year in the ground, trees benefit from partial shading (Gould 1939). After the first year of growth, if trees are over about 45 cm in height, pawpaw trees are tolerant of full sun, and mature trees will bear large quantities of fruit in an open exposure if properly pollinated. The soil should be slightly acid (pH 5.4-7.0), deep, fertile, and well-drained. Bonney (2002) found that the soil pH ranged from neutral (7.05) to acidic (5.38) in eight wild patches in Kentucky. Pawpaw trees will not thrive if frequently flooded (Nash and Graves 1993) or if they are grown in heavy soil or waterlogged soil (Lagrange and Tramer 1985). Lagrange and Tramer (1985) reported that soils in wild pawpaw patches varied considerably in sand/silt/clay ratios, although clay contents were generally low. Pawpaw trees attained their greatest height in moist sites that were characterized by occasional flooding, but with soils with a high percentage of sand and good drainage. Pawpaws are sensitive to both flooding and drought (Nash and Graves 1993). Adequate soil moisture is critical during the first two years of establishment. Mulching pawpaws with straw helps to preserve soil moisture and enhances survival. Straw mulch also produces a soft cushion to prevent bruising of fruits that may fall to the ground before hand-harvesting.

## **B.** Seedling Propagation

The pawpaw produces a relatively large seed averaging  $2.8 \pm 0.1$  cm in length and  $1.5 \pm 0.1$  cm in width (Geneve et al. 2003). The flat, spatulate seed has a dark-brown fibrous seed coat 16 cell layers thick (Corner 1948; Mohana Rao 1982). A ruminant endosperm occupies most of the seed cavity, characteristic of seeds from annonaceous species (Hayat 1963; Rizzini 1973). A small (1 mm long) embryo is located at the hilar end of the seed (Finneseth et al. 1998a).

Seed can be collected from fruit when the flesh is soft or over-ripe (Layne 1996; Hartmann et al. 2002). Pawpaw has moderately recalcitrant seed that does not tolerate desiccation, and it only has a relatively short period of viability (Bonner and Halls 1974; Finneseth et al. 1998b). Des-

yP is the percent polymorphic loci and He the mean gene heterozygosity, respectively.

<sup>\*</sup>Calculated by Huang et al. (1997) from the data published by Elstrand and Lee (1987) including three other monomorphic loci.

<sup>&</sup>quot;Calculated by Huang et al. (1997) from data published by Pascual et al. (1993) including 16 other monomorphic loci.

<sup>&</sup>lt;sup>v</sup>From Huang et al. (1997).

<sup>&</sup>lt;sup>u</sup>From Huang et al. (1998).

<sup>&</sup>lt;sup>t</sup>From Huang et al. (2000).

From Huang et al. (2003).

From Pomper et al. (2003b).

iccation of pawpaw seed reduces viability by 50% when seed moisture content declines from 37 to 25% (Finneseth et al. 1998a). As little as 5 days under open air conditions can reduce the moisture content of pawpaw seeds to 5% and result in total loss of viability. Pawpaw seeds must be stored moist at chilling (5°C) temperature to retain viability in long-term storage (Finneseth et al. 1998b). The seed can be stored in moist peat moss in ziplock bags for 2 to 3 years at 5°C and maintain a high germination percentage (Finneseth et al. 1998a). In contrast, seeds stored moist at warm (25°C) temperature will lose viability in storage after 6 months to 1 year. Storing pawpaw seed below freezing (–15°C) will kill the embryo (Pomper et al. 2000).

Pawpaw seeds also display combinational (morphophysiological) dormancy (Nikolaeva 1977) requiring a period of chilling stratification to satisfy intermediate physiological endogenous dormancy followed by a moist warm period to satisfy morphological dormancy (Finneseth et al. 1998b; Geneve et al. 2003). Pawpaw seeds need to be stratified between 60 and 120 days and this range in stratification time may reflect inherent variation found in seed collected from different locations across pawpaw's wide geographic distribution (Dirr and Heuser 1987; Reich 1991; Young and Young 1992; Finneseth et al. 1998b). Using pawpaw seeds collected from six locations within Kentucky, Finneseth et al. (1998b) determined that approximately 7 weeks of chilling (5°C) stratification was required to reach 50% germination and that the greatest germination percentage (84 to 90%) occurred after approximately 100 days of stratification.

Once endogenous dormancy is relieved, pawpaw seeds still exhibit morphological dormancy. Seeds contain either a rudimentary or linear embryo that is not fully developed at the time the seed is mature and occupies less than one-half of the seed cavity (Nikolaeva 1977; Baskin and Baskin 1998; Finneseth et al. 1998a). When stratified seeds are moved to warm conditions, the cotyledons and radicle begin to grow at nearly comparable rates (Finneseth et al. 1998a). The cotyledons grow through two specialized channels that are distinct from the rest of the endosperm, while the hypocotyl and radicle emerge from the seed coat. The expanding cotyledons eventually extend to the tip of the seed. The cotyledons appear to act as haustorial structures transferring digested materials from the endosperm to the developing radicle (Finneseth et al. 1998a). The hypocotyl and radical continues to thicken to form a taproot. Forty-five days after sowing, the epicotyl emerges from the growing substrate. At this time the taproot averages (15 cm) in length and represents approximately 75% of the dry mass of the seedling. Seedling emergence is via a hypocotyl hook, but the seed coat containing the exhausted endosperm and the haustorial cotyledons may or may not

emerge from the growing medium. In either case, the cotyledons never emerge from the seed coat and are shed along with the remnants of the seed soon after the epicotyl begins to elongate. This type of seed germination where the cotyledons emerge above the soil but remain inside the seed is described as durian germination (Ng 1973). Pawpaw can be further subdivided into the blumeodendron type of durian germination (de Vogel 1980). Pawpaw is the first non-tropical species reported with durian germination (Baskin and Baskin 1998).

Pawpaw seedlings develop a strong taproot with a fragile root system, which can be easily damaged upon digging; therefore, most nurseries propagate trees in containers (Layne 1996; Pomper et al. 2003c). Desiccation of field sown seed will greatly reduce germination rates. Recent studies have developed recommendations (e.g., potting substrate type, fertilization requirements, container size, shading, etc.) for successful container production of pawpaw (Layne 1996; Finneseth et al. 1998a; Jones et al. 1998; Pomper et al. 2002a). A well-aerated potting substrate with a high sphagnum peat moss component (>75% by volume), cation exchange capacity, and water-holding capacity can be used effectively in container production (Pomper et al. 2002b). Tall containers should be used to accommodate the developing taproot of seedlings (Pomper et al. 2003c). The slow-release fertilizer Osmocote 14-14-14 (14N-6.1P-11.6K) incorporated into Pro-Mix BX potting substrate can be used effectively as the sole fertilizer source at a treatment rate of  $2.22\ kg\ m^{-3}$  in containerized pawpaw production (Pomper et al. 2002c). It can also be used at a lower rate of 0.81 kg m<sup>-3</sup> when supplemented with weekly applications of 500 mg L<sup>-1</sup> of Peters 20-20-20 (20N-8.78P-16.6K) liquid-feed fertilizer (Pomper et al. 2002c). If pawpaw seedlings are grown for longer than 4 months with Osmocote 14-14-14 (14N-6.1P-11.6K) as the sole fertilizer source in the potting substrate Pro-Mix BX, seedlings may display micronutrient deficiency symptoms. Thus, if pawpaw seedlings are to be grown in containers with Pro-MixBX or similar peat-based substrate for longer than four months, plants should receive a one-time application of soluble trace element mix (S.T.E.M.; Scotts Co., Marysville, Ohio) at a rate of 600 mg  $\rm L^{-1}$  about 3 months after sowing. Pawpaw seedlings grown for longer than 4 months in the potting substrate Pro-MixBX may also develop calcium deficiency symptoms. One or more applications of calcium nitrate at a rate of  $500 \text{ mg L}^{-1}$  should also be provided to pawpaw seedlings at 3 months after sowing to avoid the development of calcium deficiency symptoms in plants. Bottom heating (32°C) of container-grown pawpaw seedlings results in greater lateral and total root dry weight (DW) than in seedlings grown at ambient temperature (24°C), which could increase the rate of establishment of seedlings in the field (Pomper et al. 2002b). Bottom heating of container-grown pawpaw seedlings could decrease both the time to produce a saleable plant and the cost of heating greenhouses.

Pawpaw seedlings grown outdoors appear to be sensitive to high irradiances upon emergence from the soil, and benefit from partial shading for the first year of development (Gould 1939). Seedlings produced in greenhouses do not show sensitivity to high light levels, suggesting that seedlings grown outdoors may be sensitive to ultraviolet radiation (Peterson 1991). Pawpaws are often found in the shaded forest understory. Young and Yavitt (1987) reported that proximal pawpaw leaves, which developed before the overstory forest canopy closed, were 76% smaller than distal leaves that developed after canopy closure. Growth of containerized pawpaw seedlings was positively influenced by low to moderate shading (28% or 51%) outdoors and low shading (33%) in the greenhouse, in a manner typical of that reported for other shadepreferring plants (Pomper et al. 2002a). Shading increased leaf chlorophyll a and b concentrations for pawpaw seedlings grown outdoors, while it decreased average specific leaf DW (mg leaf DW cm<sup>-2</sup>). Low to moderate shading of pawpaw seedlings grown outdoors greatly increased whole plant biomass, indicating that commercial nurseries could possibly enhance production of containerized pawpaw seedlings using this shading regime outdoors. If plants are produced on a gravel container pad, higher levels of shading (>55%) that would also reduce air temperatures could be beneficial.

Pomper et al. (2002a) reported that application of  $\text{Cu(OH)}_2$  to the interior of Rootrainers (0.7 L) did not promote development of a more fibrous root system in pawpaw seedlings as reported for other tree species, based on failure of copper compound to increase lateral root dry weight production. In shaded plants, seedlings showed yellowing of leaves and reduced chlorophyll levels by the end of the experiment, suggesting that the plants were suffering from copper toxicity. However, the use of larger containers (8 L) with  $\text{Cu(OH)}_2$  applied to the interior of containers does increase seedling lateral root dry weight.

# C. Clonal Propagation

Propagation by rooting of stem cuttings is difficult in pawpaw and is not currently a viable commercial practice. Experiments using cuttings taken from seedlings of various ages showed a significant impact of juvenility on pawpaw rooting ability. In a systematic study using over 1200 stem cuttings taken from mature flowering pawpaw trees at 7-day intervals

from 17 June to 5 August only one cutting produced an adventitious root (Finneseth 1997). Cuttings taken from up to 2-month-old seedlings showed a high capacity to root. Cuttings treated with 10,000 mg L<sup>-1</sup> IBA rooted at 75% and averaged two roots per cutting (Geneve et al. 2003). Seedlings beyond 2 months showed a reduced capacity to form roots. Cuttings taken from 7-month-old seedlings rooted at less than 10% regardless of auxin treatment. Strategies to revert stock plants to a more juvenile state (i.e., tissue culture or mound layering) may be required before a reliable method for cutting propagation can be obtained.

Pawpaw is a naturally suckering species, readily forming adventitious shoots from roots. Propagation from root cuttings can be an alternative method for multiplication of difficult-to-root species such as pawpaw. Shoots derived adventitiously from roots retain a juvenile character and could serve as a source for stem cuttings or explants for tissue culture (Hackett 1985). Finneseth (1997) collected root cuttings from a wild patch in December in Kentucky, and found no shoots formed on root pieces that were less than 5 mm in diameter, while 56% of root pieces greater than 5 mm in diameter produced one or more shoots. On average, responding roots produced 2.5 buds and 1.1 elongating shoots. Buds were visible on root pieces 12 weeks after planting and shoot elongation was evident after 16 weeks. Stooling (mound layering) has been attempted in the field as a method to propagate pawpaw selections. In a factorial experiment with two levels of girdling (girdled or not) and three levels of IBA at 0, 3000, and 6000 mg L<sup>-1</sup> in lanolin paste, only two roots formed on one shoot out of 80 treated shoots (Pomper, unpubl. data).

Pawpaws are easily propagated by grafting and budding (e.g., whip-and-tongue, cleft, bark inlay, and chip budding) (Layne 1996). Winter collected, dormant budwood should have its chilling requirement fulfilled. The whip-and-tongue graft of a scion to an actively growing root-stock is used by several commercial nurseries to propagate pawpaw cultivars. Chip budding is most successful when the seedling rootstock is at least 0.5 cm diameter and actively growing. Bud take exceeding 90% can be obtained.

Currently, pawpaw cultivars with superior fruit characteristics are propagated by grafting and budding onto seedling rootstocks. Seedling rootstock research has used seed from open-pollinated half-sib trees at the Keedysville orchard at the Western Maryland Research and Education Center. Great variation in scion growth has been observed in orchards at KSU when these seedlings have been used as rootstock (Pomper et al. 2003d). Seedstock from various pawpaw genotypes are

currently being screened to identify seedling rootstocks that could result in improved pawpaw establishment rates and precocity.

Micropropagation of pawpaw has not been successful. In establishment studies, seedling nodal explants of pawpaw responded more favorably than apical sections for establishment (Finneseth 1997; Geneve et al. 2003). When nodal explants were treated with a range of benzyladenine (BA) concentrations (0, 5, 10, or 15 μM) on MS medium, fewer than 0.5 shoots developed per explant (Finneseth 1997). However, when seedling explants were treated with 1.0 µM thidiazuron (TDZ) plus 10 um BA, all cultures produced over 1.0 shoot per culture. Explant establishment from seedling, mature, or rejuvenated sources was attempted using Murashige and Skoog (MS) medium (Murashige and Skoog 1962) supplemented with 10 μM BA plus 0.1 μM TDZ (Finneseth et al. 2000). A small number of mature explants survived and produced a limited number of shoot buds after 7 months in culture. However, these never stabilized and no mature cultures survived for more than 12 months in culture. Bellini et al. (2003) has reported difficulty in disinfesting pawpaw explants collected in the field, with cultures being lost to contamination by fungal and bacterial organisms.

Geneve et al. (2003) reported one pawpaw accession (A10-11) developed from rejuvenated explant sources showed continued growth and shoot production during subculturing. It has been maintained in culture for over 3 years. The ability for single stem explants from 3-year-old cultures of A10-11 to support shoot multiplication was investigated using 9.8 им IBA plus 5.4 им NAA in combination with BA (0 to 20 им). Initial explants elongated but did not form additional shoots after 8 weeks in culture (J. Egilla, unpubl.). These were subcultured to the same medium and after 9 weeks cultures treated with 15 or 20 µm BA had the greatest number of shoots per culture and 15 µM BA had the most vigorous shoot growth. These data indicate that cultures of pawpaw can retain morphogenetic potential for a considerable time in culture. Preliminary experiments to root microcuttings of pawpaw have met with little success (S. T. Kester and R. L. Geneve, unpubl.). In these experiments, microshoots were developed from pawpaw cultures maintained for over 2 years. The original explants were shoots developed on root pieces from the A10-11 understock. Initial treatments placing explants on one-half strength MS salts medium containing IBA (0.49 to 4.9  $\mu$ M) resulted in a small percentage (3.0%) of microcuttings developing one to two roots per cutting at the 4.9 µM IBA level. However, these rooted shoots did not thrive during the acclimatization stage and failed to develop further.

## D. Orchard Establishment and Training

Poor establishment rates have been a problem in pawpaw orchards. Establishment and survival of trees in the PRVT has varied between 10% to 95% survival rates (Merwin et al. 2003; Pomper et al. 2003d; Postman et al. 2003). Generally, trees that are 45 to 90 cm at planting have a lower mortality rate than smaller trees. Tree establishment and survival was enhanced when trees were grown in copper treated 8 L containers (K. W. Pomper, unpubl. data).

Present recommendations for pawpaw plantings are 2.4 m within rows and 3.7 to 4.6 m between rows. During the first year of establishment, pawpaw trees show little growth and can have an early leaf drop the first fall. For the first two years, top growth is slow as the root system establishes itself, but thereafter it accelerates substantially given proper fertility and soil moisture. Row orientation should be north-south if possible.

Shading of pawpaw in the field the first year is recommended and can be accomplished by installing translucent double-walled polyethylene "tree-tubes" around each tree, securing them with bamboo stakes (Layne 1996). However, trees taller than 45 cm at planting do not require shading. During warm summer temperatures (>35°C), the tubes should be removed from the trees, otherwise foliage within tubes can became heat-stressed and desiccated. In New York, open mesh black plastic trunk guards provided adequate shade and protection for newly planted pawpaw trees, whereas translucent plastic tree-tubes caused heat stress and scorching of the young trees (Merwin et al. 2003).

Weed control is important to improve establishment, but there are no herbicides currently labeled for use on pawpaw. Mulching around trees with wood chip mulch (15 cm depth) or with straw can be an effective method of weed control for at least one year and possibly two. However, this is a labor-intensive method, and may be cost prohibitive. Weed mats or landscape fabric can control weeds for up to 3 years and assist in water conservation. Irrigation during establishment improves tree survival rates, but irrigation requirements of pawpaw have not been determined. Trickle irrigation with emitters that provided 3.8 L/hr with 2 emitters/tree for a total of about 945 L/tree per year has given good results.

Fertilization requirements have not been determined yet for bearing pawpaw trees. Trees fertigated with water-soluble fertilizer (20N-8.6P-16.6K) plus soluble trace elements once in May, June, and July during active growth in Kentucky have achieved 30 to 45 cm of shoot extension

each year. Excellent growth has been achieved with granular ammonium nitrate fertilizer (34-0-0) broadcast under pawpaw trees in early spring at  $30-60~\rm g~N/tree$  applied before budbreak.

High-sodium conditions are potentially damaging to salt-sensitive fruit crops (Picchioni et al. 1990, 2000; Picchioni and Graham 2001). Thus, the intrinsic difficulties in field transplanting *A. triloba* (Callaway 1990) could be increased with sodium stress. For a southern *A. triloba* ecotype exposed to high-sodium conditions, the addition of gypsum improves field growth and survival rates, and increases fertilizer-N recovery during early orchard establishment (Picchioni et al. 2004).

Most pawpaw genotypes naturally develop a strong central leader. Branches can often develop sharp crotch angles in relation to the trunk. Trees should not be headed at planting and no pruning is required the first year. Pruning is conducted in late winter-early spring and consists of removing low branches to a height 60 to 90 cm on the trunk. Training to more horizontal scaffold limbs increases scaffold strength and reduces limb breakage which may occur under heavy crops.

## E. Flowering, Fruit Set, and Yield

Flowers are strongly protogynous and are likely self-incompatible (Willson and Schemske 1980), although 'Sunflower' may be self-fruitful. Pollination is by flies (Diptera) and beetles (Nitidulidae), and possibly other nocturnal insects (Kral 1960; Faegri and van der Pijl 1971; Willson and Schemske 1980). Seedlings normally begin to flower when they reach a height of about 1.8 m, but may not set fruit; cropping is achieved at five to eight years. Grafted pawpaw trees often flower within 3 years after planting, but often fail to set fruit (Bratsch et al. 2003; Merwin et al. 2003; Pomper et al. 2003d). Failure of trees to set fruit could be due to inadequate pollination or inadequate canopy to support fruit development. Usually 5 to 6 years are required for grafted trees to begin production, although some cultivars such as 'PA-Golden (#1)' may produce crops 4 to 5 years after planting (Pomper et al. 2003d).

The normal bloom period for pawpaw may last from 3 to 4 weeks. Thus, harvest is often extended over a similar time frame. Each fruit cluster develops from an individual flower, and fruit within a cluster often ripen at different times (Fig. 7.1). In the spring of 2002, flowering, fruit set, fruit drop, and ripening characteristics were examined in six-year-old trees for 'PA-Golden (#1)', 'Wilson', and 'Sunflower' in Kentucky. The flowering period of individual trees for each cultivar extended from

April 15 until May 1! but 75% of all flowers bloomed from April 15 until May 1. Half of theres of each cultivar examined in 2002 dropped about 50% of their cluters between May 8 and July 11. The average fruit set was 25% and this presponded to 21, 9, and 7 fruit clusters per tree for 'PA-Golden', 'Wilsn', and 'Sunflower', respectively. Fruit ripening periods for all cultivas reflected the long flowering periods of the cultivars. Harvest period extended from August 20 to September 6 for 'PA-Golden', from Agust 22 to September 9 for 'Wilson', and from August 23 to Septembr 21 for 'Sunflower'.

In cultivation, pawaw yields per tree are often low (Peterson 1991). For the cultivars in the above 2002 study, yield averaged 6.4, 2.0, and 3.7 kg per tree for 'PAGolden', 'Wilson', and 'Sunflower', respectively. In another study, yiels per tree in the 7th year were: 4.4 kg for 'Sunflower', 2.3 kg for 8-2(and 2.2 kg for 'PA-Golden' (Pomper et al. 2003d). The tropical Annonaeae relatives of the pawpaw, such as cherimoya, sweetsop (sugar apple, soursop, and atemoya also have low yields, due to low rates of natura pollination (Peterson 1991; George et al. 1992; Pena et al. 1999). In cmmercial plantings, these tropical pawpaw relatives are hand pollined to increase yields (Peterson 1991; Pena et al. 1999). Low rates (<5°) of fruit set have also been noted in wild pawpaw patches (Willsomnd Schemske 1980; Lagrange and Tramer 1985).

In the wild, pawpw trees are usually found in the understory of hardwood forests. Lev light levels in the understory likely result in reduced photosyntha: partitioning to fruit that may cause low fruit set. Pawpaws in the wild ften produce many root suckers that could potentially result in large clnal pawpaw patches contributing to poor fruit set because of self-incomatibility. Pollinator limitation can also cause low fruit set in wild pawaw patches (Willson and Schemske 1980). Low pollinator activity is rually observed on cool, cloudy spring days. Since the pawpaw flowers re strongly protogynous (Willson and Schemske 1980), lack of pollen vailability from other pawpaw genotypes could also limit pollinatior Pawpaw growers report that placing carrion in buckets among pawpw trees has resulted in improvements in fruit set (L. Sibley, pers. comn.) supporting the theory that pawpaw flowers may be pollinated by:arrion flies. However, fruit set was 15 to 35% in KSU orchards in 199 in nine-year-old seedlings where many pawpaw genotypes are in clos proximity and flies are abundant due to nearby cattle. Pollinizer relaionships between pawpaw cultivars need to be determined. Fruit setan be achieved by hand cross-pollination (Peterson 1997), and needsto be evaluated as a method to increase fruit set.

# F. Fruit Ripening and Postharvest Physiology

The primary impediment to introduction of pawpaw into both fresh and processing markets is its perishability (Popenoe 1916, 1917; Peterson 1991). In order to facilitate the growth of a commercial pawpaw industry, several problems with harvest and postharvest handling of fruit will need to be resolved.

Pawpaw fruit ripening is characterized by an increase in soluble solids concentration (up to 20%), flesh softening, increased volatile production, and, in some genotypes, a decline in green color intensity (McGrath and Karahadian 1994). The volatile profile during ripening consists primarily of ethyl and methyl esters (Shiota 1991; McGrath and Karahadian 1994). Within 3 days after harvest, ethylene and respiratory climacteric peaks are clearly evident as pawpaw fruit rapidly soften (Archbold et al. 2003; Archbold and Pomper 2003; Koslanund 2003). Other members of the Annonaceae such as cherimoya, sweetsop (sugar apple), soursop, and atemoya, are also climacteric (Biale and Barcus 1970; Kosiyachinda and Young 1975; Paull 1982; Wills et al. 1984; Brown et al. 1988). Fruit of these tropical species exhibit similar climacteric maxima, although some have two respiratory peaks. Preliminary analyses conducted by Koslanund (2003) indicate that the decline in firmness of pawpaw fruit is due to the action of at least four enzymes: polygalacturonase, cellulase, pectin methylesterase, and endo-β-mannanase.

Color change is generally not a reliable indicator of pawpaw fruit ripeness. Although a decline in green color intensity during pawpaw ripening has been reported by McGrath and Karahadian (1994), we have found that it is not consistent among genotypes, occurs later in ripening if at all, and is not easy to identify visually. A common practice to determine maturity is to touch each fruit to determine if it is ready to harvest; ripe softening pawpaw fruit yield to slight pressure, as ripe peaches do, and can be picked easily with a gentle tug. Thus, fruit are harvested when they have already begun ripening and have lost some firmness. This is labor intensive and may result in slight bruising injury, perhaps leading to off-flavors (Peterson 1991). Also, a natural abscission zone forms where the fruit attaches to the peduncle when fruit ripen. "Wiggling" the fruit can determine how well this abscission zone has formed. Ripening fruit also give off a strong aroma. Fruit on a single tree do not ripen within close proximity in time to one another. An extended harvest period of two weeks or longer from an individual tree is not uncommon. The protracted harvest may be due in part to the staggered bloom period in the spring, but it is not known if the bloom to harvest period is the same for all fruit on a tree. Although each fruit cluster develops from an individual flower, fruit within a cluster often ripen at different times. Currently, multiple harvests from one tree are conducted to obtain high-quality fruit. Cultivar variation in harvest period also exists. Because of the lack of easily identifiable ripening traits, it is difficult to determine fruit maturity except by individual "feel" or to determine softening. Softer fruit needs to be marketed immediately, while firmer fruit should be held in cold storage at 4°C.

Pawpaw fruit soften rapidly at room temperature after harvest. McGrath and Karahadian (1994) and Layne (1996) indicated a 2- to 3-day shelf life, although fruit that are just beginning to soften have a 5-to 7-day shelf life (Archbold et al. 2003) at room temperature. However, we have observed that pawpaw fruit can be stored for 1 month at 4°C with little change in fruit firmness; fruit then ripen upon removal to ambient temperature. The optimum temperature and duration for holding the fruit needs to be determined. Immature fruit does not ripen, even if treated with ethephon at 1000 mg L<sup>-1</sup>. Controlled or modified atmosphere storage has not been evaluated. Fruit packaging needs to be developed to minimize bruising. Because fruit is non-uniform in size and shape, packing for shipping presents some unique challenges.

## G. Medicinal and Pesticidal Uses

Annonaceous acetogenins have been extracted from pawpaw twigs and have potential as medications and pesticides (Zhao et al. 1994; Johnson et al. 1996; McLaughlin 1997; McCage et al. 2002). About 250 of these compounds have been isolated and characterized (McLaughlin 1997). Three compounds—bullatacin, bulletin, and bullanin—have high potencies against human solid tumor cell lines in vitro (Zhao et al. 1994). Several acetogenins have been patented for pesticidal use (McLaughlin 1997) and as anti-tumor agents (Zhao et al. 1994; McLaughlin 1997). Another patented product made from annonaceous acetogenins is a head lice remover shampoo developed by Jerry McLaughlin of Nature's Sunshine Products [Spanish Fork, Utah; patents 4,721,727, 4,855,319, and 09/213,164 (pending); United States Patent and Trademark Office, www.uspto.gov] (McCage et al. 2002). Botanically-derived pesticides that are environmentally compatible and biologically degradable may be obtained from pawpaw (Ratnayake et al. 1993). Pests are less likely to develop resistance to botanically-derived pesticides, as they often have a larger pesticidal spectrum (Arnason et al. 1989). Asimicin, extracted from pawpaw, has been shown to have significant pesticidal activity against mosquito larvae (Aedes aegypti L.), blowfly larvae (Colliphora vicina Meig), two-spotted spider mite (Tetranychus urticae Koch),

striped cucumber beetle (*Acalymma vittatum* F.), melon aphid (*Aphis gossyphii* Glover), Mexican bean beetle (*Epilachna varivestis* Mulsant), and a free-living nematode [*Caenorhabditis elegans* (Maupas) Dougherty] (Alkofahi et al. 1989).

A market exists for biomass produced by growers to supply annonaceous acetogenins for the production of pawpaw products such as head lice remover shampoo. Acetogenin concentration varies monthly in pawpaw tree tissues, being highest in the spring and summer months (Johnson et al. 1996). However, pawpaw twigs can be harvested, dried, ground, and then stored for later extraction (Johnson et al. 1996).

# H. Disease and Pest Management

Pawpaws have few disease problems. Pawpaw leaves can exhibit leaf spot, principally a complex of Mycocentrospora aiminae, Rhopaloconidium asiminae Ellis & Morg., and Phyllosticta asiminae Ellis & Kellerm (Farr et al. 1989; Peterson 1991) and some trees in the PRVT planting in Frankfort, Kentucky have exhibited signs of these foliar diseases. The pawpaw peduncle borer (Talponia plummeriana Busck) is a small moth larva, about 5 mm long, that burrows into the fleshy tissues of the flower, causing the flower to wither and drop (Heinrich 1926; MacKay 1959; Peterson 1991). Signs of the pawpaw peduncle borer have been observed in pawpaw orchards in Maryland (R. N. Peterson, pers. commun.), but not in Kentucky. The zebra swallowtail butterfly (Eurytides marcellus), whose larvae feed exclusively on young pawpaw foliage, will damage leaves, but this damage has been negligible at the PRVT plantings. The larvae of the leafroller (Choristoneura parallela Robinson) may damage flowers and leaves (Norman et al. 1992). Deer will not generally eat the leaves or twigs, but they will eat fruit that has dropped on the ground. Male deer may rub trees with their antlers breaking branches. Japanese beetles (Popillia japonica Newman) can damage young leaves on pawpaw trees.

## I. Tree Decline

Pawpaw trees usually survive for 20 years or more; however, tree decline may be a problem in some pawpaw orchards. About 1% of trees in the PPF orchard at Queenstown, Maryland die annually from an unidentified decline. Grafted pawpaw trees do not survive as long as seedling trees, suggesting rootstock/scion incompatibility could result in tree decline and death (G. Reighard, Clemson University, pers. commun.).

Rootstock produced from seed from the same scion may be more compatible and promote long-term survival of grafted trees.

Vascular wilt-like symptoms have been observed in the spring after pawpaw trees leafed out in orchards in Oregon (Postman et al. 2003), North Carolina (M. Parker, North Carolina State University, pers. commun.), and Maryland (N. Peterson, pers. commun.). As transpiration demand increased with warmer and drier weather, severely affected trees collapsed and died. Moderately affected trees became chlorotic with stunted new growth. Blue and black vascular discoloration was observed beneath the bark of declining trees along the lower parts of the main stem, particularly at and above the graft unions. This symptom has been described as "blue-stain." A canker-like bark splitting was also observed near the base of many declining trees, with smaller cankers on upper scaffold branches. Several species of fungi in the genera Ceratocystis and Leptographium have been associated with "blue-stain" in conifer timber, and a few species are associated with tree diseases. In most cases, spread of these fungi has been attributed to assorted bark beetles or other insects (Sohlheim and Safranyik 1997; Jacobs et al. 2000; Jacobs and Wingfield 2001). Blue discoloration beneath the bark of pawpaw trees seems to be a common response of this host to injury and may be associated with more than one disease or disorder. A PRVT that was established at the USDA-NCGR in Corvallis, Oregon,

in the fall of 1995 has had difficulties with high tree mortality. Postman et al. (2003) reported that two years after planting, 13% of trees had either failed to establish or had died after an initial healthy start. By July 1999, 25% of grafted trees had died due to a vascular wilt-like disease, and 2 years later mortality exceeded 50%. Seedling guard trees were unaffected until July 2000, when six guard trees of 76 died and 10 more were declining. By July 2001, 14 guard trees were dead. No fungi were consistently isolated from declining trees. A number of bacteria were isolated from infected trees, but no specific pathogen has been confirmed as the causal agent. Polymerase chain reaction (PCR) tests for phytoplasmas and for the bacterium Xylella fastidiosa were also negative. Research is ongoing to determine if a bacterial pathogen was the cause of the pawpaw decline. Despite the vascular wilt-like disease in this plot, healthy, producing pawpaw trees have been growing for more than 20 years at several gardens in Oregon's Willamette Valley (J. Postman, pers. commun.). The demise of the NCGR Corvallis PRVT may help to identify sources of resistance to this as yet

unidentified disease. Trees in the PPF orchard at Queenstown, Maryland

have exhibited similar disease symptoms to those in Oregon, but as stated

previously only about 1% die annually (N. Peterson, pers. commun.).

## J. Marketing and Consumer Acceptance

The taste and aroma of overripe pawpaw fruit can be very strong and possibly objectionable to some consumers. Pawpaw fruit can also be seedy. Although there are no seedless pawpaw fruit currently available, superior genotypes have about 5 to 10% seed on a fresh weight basis. Ripe pawpaw fruit are similar in appearance to mango and papaya fruit, and if handling avoids bruising, have a similar fresh market appeal.

Pawpaw fruit have significant processing potential but commercial pulp extraction methods have not been examined. Langworthy and Holmes (1917) observed that the pawpaw fruit was little known outside of regions where it is found, but deemed it worthy of further study because of its distinctive flavor. In a consumer acceptance study conducted at a 1999 pawpaw field day (Templeton et al. 2003), pawpaw ice cream was the best-received item (55% of tasters liked it extremely), followed by pawpaw cake with lemon icing, liked extremely by 45%. The pawpaw/grape juice drink was liked extremely by 31% of participants. Plain pawpaw butter was liked extremely by 26% of tasters; pawpaw butter prepared with lemon and grape juice was liked extremely by 11%, while the version prepared with orange and lemon was liked extremely by only 8%. The custard prepared from ripe, mild-flavored fruit was liked extremely by 42% of tasters, while the custard prepared from mixed under-ripe, over-ripe, and bruised fruit was liked extremely by only 16%. Overall, the positive acceptance of pawpaw products by tasters demonstrates the potential of commercial processing ventures.

Wiese and Duffrin (2003) investigated the sensory properties of plain shortened cake using pawpaw fruit puree as a partial replacement for fat in the food formulation. The influence on the color, texture, and tenderness appeared to influence the preference ratings for the category of overall acceptability. Participants preferred the no pawpaw pulp control and 25% samples to 50% and 75% of the fat replacement with pawpaw fruit puree. The 50% and 75% replacement of fat with pawpaw fruit puree in the cake samples resulted in a reduced preference for the categories of color, texture, tenderness, and overall acceptability. In examining a muffin formulation, Duffrin et al. (2001) also found that some fat is required in a food formulation along with pawpaw fruit puree for a desirable product. The custard-like texture of the pawpaw fruit, its nutrient composition, and acceptance by tasters make it an excellent candidate as at least a partial fat-reducing agent in baked goods. Jones and Layne (1997) noted that most dessert recipes requiring banana could have equal part substitution with pawpaw puree and be very acceptable.

#### V. FUTURE PROSPECTS

The unique qualities of the fruit, ornamental value of the tree, and the natural compounds in the leaf and bark suggest that pawpaw has great potential as a new crop. However, there are many challenges, including developing a grower base, improving orchard establishment rates, rootstock development, improving clonal propagation methods, new cultivar development, increasing yields, postharvest handling of fruit, and developing an overall marketing strategy.

### LITERATURE CITED

Alkofahi, A., J. K. Rupprecht, J. E. Anderson, J. L. McLaughlin, K. L. Mikolajczak, and B. A. Scott. 1989. p. 25–43. In: J. T. Arnason, B. J. R. Philogene, and P. Morand (eds.), Insecticides of plant origin: Search for new pesticides from higher plants. Am. Chem. Soc. Washington, D.C.

Archbold, D. D., R. Kosnalund, and K. W. Pomper. 2003. Ripening and postharvest storage of pawpaw. HortTechnology 13:439–441.

Archbold, D. D., and K. W. Pomper. 2003. Ripening pawpaw fruit exhibit respiratory and ethylene climacterics. Post. Biol. Tech. 30:99–103.

Arnason, J. T., B. J. R. Philogene, and P. Morand. 1989. Preface. p. ix–x. In: Insecticides of plant origin. J. T. Arnason, B. J. R. Philogene, and P. Morand (eds.) Am. Chem. Soc. Washington, DC.

Bailey, L. H. 1960. The standard cyclopedia of horticulture, Vol. I. Macmillan Co., New York.

Barber, M. A. 1905. Poisoning due to papaw (Asimina triloba). J. Am. Med. Assoc. 45:2013–2014.

Bartholomew, E. A. 1962. Possibilities of the pawpaw. Northern Nut Growers Assn. Ann. Rep. 53:71–74.

Baskin, C. C., and J. M. Baskin. 1998. Seeds. Ecology, biogeography, and evolution of dormancy and germination. Academic Press, New York.

Bellini, E., S. Nin, and M. Cocchi. 2003. The pawpaw research program at the horticulture department of the University of Florence. HortTechnology 13:455–457.

Biale, J. B., and D. E. Barcus. 1970. Respiration patterns in tropical fruits of the Amazon basin. Trop. Sci. 12:93–104.

Bonner, F. T., and L. K. Halls. 1974. *Asimina Adans.*—Pawpaw. [Seed production] U.S. Dept. of Agr. Agr. Handb. 450:238–239.

Bonney, T. M. 2002. Development of a sampling strategy and random amplified polymorphic DNA (RAPD) protocol for genetic analysis of the North American pawpaw [Asimina triloba (L.) Dunal]. M.S. Thesis, Dept. Horticulture, Univ. Kentucky, Lexington.

Bowden, W. M. 1948. Chromosome numbers in the *Annonaceae*. Am. J. Bot. 35:377–381. Bowden, W. M. 1949. Triploid mutants among diploid seedling populations of *Asimina triloba*. Bul. Torrey Bot. Club 76:1–6.

Bratsch, A., R. Bellm, and D. Kniepkamp. 2003. Early growth characteristics of seven grafted varieties and non-grafted seedling pawpaw. HortTechnology 13:423–427.

- Brown, B. I., L. S. Wong, A. P. George, and R. J. Nissen. 1988. Comparative studies on the postharvest physiology of fruit from different species of *Annona* (custard apple). J. Hort. Sci. 63:521–528.
- Callaway, M. B. 1990. The pawpaw (Asimina triloba). Kentucky State Univ. Pub. CRS-HORT1-901T.
- Callaway, M. B. 1992. Current research for the commercial development of pawpaw [Asimina triloba (L.) Dunal]. HortScience 27:90, 191.
- Callaway, M. B. 1993. Pawpaw (*Asimina triloba*): A "tropical" fruit for temperate climates. p. 505–515. In: J. Janick and J. E. Simon (eds.), New crops. Wiley, New York.
- Conquist, A. 1981. An integrated classification of flowering plants. Columbia Univ. Press, New York.
- Corner, E. H. J. 1948. The Annonaceous seed and its four integuments. New Phytol. 48: 332–364.
- Damman, A. J. 1986. Effects of seasonal changes in leaf quality and abundance of natural enemies on the insect herbivores of pawpaw. Ph.D. Dissertation, Cornell Univ., Ithaca, N.Y.
- Darrow, G. M. 1975. Minor temperate fruits. p. 276–277. In: J. Janick and J. N. Moore (eds.), Advances in fruit breeding. Purdue Univ. Press, West Lafayette, IN.
- de Vogel, E. F. 1980. Seedlings of dicotyledons. Centre Agr. Pub. Doc. Wageningen, The Netherlands.
- Dirr, M. A. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 4th ed. Stipes Publ. Co., Champaign, IL.
- Dirr, M. A., and C. W. Heuser. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Varsity Press, Athens, GA.
- Duffrin, M. W., D. H. Holben, and M. J. Bremner. 2001. Consumer acceptance of pawpaw (*Asimina triloba*) fruit puree as a fat-reducing agent in muffins, compared to muffins made with applesauce and fat. Family Consumer Sciences Res. J. 29:281–287.
- Ellstrand, N. C., and J. L. Lee. 1987. Cultivar identification of cherimoya (*Annona cherimola* Mill.) using isozyme markers. Scientia Hort. 32:25–31.
- Faegri, K., and L. van der Pijl. 1971. The principles of pollination ecology, p. 112–122.

  Pergamon, New York.
- Farr, D. F., G. F. Bills, G. P. Chamuris, and A. Y. Rossmoan. 1989. Fungi on plants and plant products in the United States. APS Press, St. Paul, Minn.
- Filson, J. 1784. The discovery, settlement, and present state of Kentucke. Originally published in Wilmington, Delaware. Republished in 1966 as part of the Great Americana Series, Readex Microprint Corp., Chester, VT.
- Finneseth, C. H. 1997. Propagation of the North American pawpaw [Asimina triloba (L.) Dunal]. M.S. Thesis, Dept. Horticulture, Univ. Kentucky, Lexington.
- Finneseth, C. H., D. R. Layne, and R. L. Geneve. 2000. Establishment of North American pawpaw [Asimina triloba (L.) Dunal] shoots in vitro from mature and juvenile explants. Acta Hort. 520:97–102.
- Finneseth, C. H., D. R. Layne, and R. L. Geneve. 1998a. Morphological development of the North American pawpaw [Asimina triloba (L.) Dunal] during germination and seedling emergence. HortScience 33:802–805.
- Finneseth, C. H., D. R. Layne, and R. L. Geneve. 1998b. Requirements for seed germination in North American pawpaw [Asimina triloba (L.) Dunal]. Seed Sci. Technol. 26: 471–480.
- Geneve, R. L., K. W. Pomper, S. T. Kester, J. N. Egilla, C. L. H. Finneseth, S. B. Crabtree, and D. R. Layne. 2003. Propagation of pawpaw—a review. HortTechnology 13:428–433.
- George, A. P., R. J. Nissen, and J. A. Campbell. 1992. Pollination and selection in *Annona* species (cherimoya, atemoya, and sugar apple). Acta Hort. 321:178–185.
- Gould, H. 1939. The native pawpaw. U.S. Dept. of Agr., Lflt. 179. Washington, D.C.

- Hackett, W. P. 1985. Juvenility, maturation, and rejuvenation in woody plants. Hort. Rev. 7:109–155.
- Hamrick, J. L., and M. J. W. Godt. 1989. Allozyme diversity in plant species, p. 43–63. In A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.), Plant population genetics, breeding and genetic resources. Sinauer Associates, Sunderland, Mass.
- Haribal, M., and P. Feeny. 1998. Oviposition stimulant for the zebra swallowtail butterfly, *Eurytides marcellus*, form the foliage of pawpaw, *Asimina triloba*. Chemoecology 8:99–110.
- Hartmann, H. T, D. E. Kester, F. T. Davies, Jr., and R. L. Geneve. 2002. Plant propagation: Principles and practices. 7th edition. Prentice Hall, Saddle River, NJ.
- Hayat, M. A. 1963. Morphology of seed germination and seedling in *Annona squamosa*. Bot. Gaz. 124:360–362.
- Heinrich, C. 1926. Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae. U.S. Natl. Museum Bul. 132.
- Huang, H., D. R. Layne, and R. N. Peterson. 1997. Using isozyme polymorphisms for identifying and assessing genetic variation in cultivated pawpaw [Asimina triloba (L.) Dunal]. J. Am. Soc. Hort. Sci. 122:504–511.
- Huang, H., D. R. Layne, and D. E. Riemenschneider. 1998. Genetic diversity and geographic differentiation in pawpaw [Asimina triloba (L.) Dunal] populations from nine states as revealed by allozyme analysis. J. Am. Soc. Hort. Sci. 123:635–641.
- Huang, H., D. R. Layne, and T. L. Kubisiak. 2000. RAPD Inheritance and diversity in paw-paw [Asimina triloba (L.) Dunal]. J. Am. Soc. Hort. Sci. 125:454–459.
- Huang, H., D. R. Layne, and T. L. Kubisiak. 2003. Molecular characterization of cultivated pawpaw [Asimina triloba (L.) Dunal] using RAPD markers. J. Am. Soc. Hort. Sci. 128: 85–93.
- Jacobs, K., M. J. Wingfield, and D. R. Bergdahl. 2000. New Leptographium species from Indonesia and eastern North America. Mycoscience 41:595–606.
- Jacobs, K., and M. J. Wingfield. 2001. *Leptographium* species: Tree pathogens, insect associates and agents of blue-stain. Phytopathology 91(6 supplement):S113.
- Johnson, H. A., J. Gordon, and J. L. McLaughlin. 1996. Monthly variations in biological activity of *Asimina triloba*. p. 609–614. In: J. Janick (ed.), Progress in new crops. ASHS Press, Arlington, VA.
- Jones, S. C., and D. R. Layne. 1997. Cooking with pawpaws. Kentucky State University Cooperative Extension Program, Bul. #PIB-001.
- Jones, S. C, R. N. Peterson, T. Turner, K. W. Pomper, and D. R. Layne. 1998. Pawpaw planting guide: Cultivars and nursery sources. Kentucky State Univ. Cooperative Extension Program, Bul. #PIB-002.
- Kosiyachinda, S., and R. E. Young. 1975. Ethylene production in relation to the initiation of respiratory climacteric in fruit. Plant Cell Physiol. 16:595–602.
- Koslanund, R. 2003. Ethylene production, fruit softening, and their manipulation during pawpaw ripening. Ph.D. Diss., Univ. Kentucky, Lexington.
- Kral, R. 1960. A revision of *Asimina* and *Deeringothamnus* (*Annonaceae*). Brittonia 12: 233–278.
- Lagrange, R. L., and E. J. Tramer. 1985. Geographic variation in size and reproductive success in the paw paw (*Asimina triloba*). Ohio J. Sci. 85:40–45.
- Langworthy, C. F., and A. D. Holmes. 1917. The American papaw and its food value.

  J. Home Econ. 9:39-45.
- Lawson, J. 1709. (Reprinted in 1967.) The natural history of Carolina. p. 111. In: H. T. Lefler (ed.), A new voyage to Carolina. Univ. North Carolina Press, Chapel Hill, NC.
- Layne, D. R. 1996. The pawpaw [Asimina triloba (L.) Dunal]: A new fruit crop for Kentucky and the United States. HortScience 31:777–784.

Layne, D. R. 1997. Pawpaws. p. 403–404. In: Register of Fruit and Nut Varieties, Third Edition. ASHS Press, Alexandria, VA.

Lewis, M., and W. Clark. 1806. (Reprinted in 1981.) In: B. DeVoto (ed.), The journals of Lewis and Clark. Houghton Mifflin Co., Boston.

Little, J. A. 1905. A treatise on the pawpaw. O. G. Swindler, Clayton, IN.

MacKay, J. W. 1959. Variat in papaw. Northern Nut Growers Assn. Ann. Rep. 66:53-55.

McGrath, M. J., and C. Karahadian. 1994. Evaluation of physical, chemical, and sensory properties of pawpaw fruit (Asimina triloba) as indicators of ripeness. J. Agr. Food Chem. 42:968-974.

McCage, C. M., S. M. Ward, C. A. Paling, D. A. Fisher, P. J. Flynn, and J. L. McLaughlin. 2002. Development of paw paw herbal shampoo for the removal of head lice. Phytomedicine 9:743-748.

McLaughlin, J. L. 1997. Anticancer and pesticidal components of pawpaw (Asimina triloba). Ann. Rep. Northern Nut Growers Assoc. 88:97-106.

Merwin, I. A., R. Byard, and K. W. Pomper. 2003. Survival, growth, and establishment of grafted pawpaws in upstate New York. HortTechnology 13:421-422.

Mohana Rao, P. R. 1982. Seed and fruit anatomy in Asimina triloba, with a discussion of the affinities of Annonaceae. Bot. Jahrb. Syst. 103:47-57.

Murashige, T., and F. Skoog. 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plant. 15:473-497.

Nash, L. J., and W. R. Graves. 1993. Drought and flood stress effects on plant development and leaf water relations of five taxa of trees native to bottomland habitats. J. Am. Soc. Hort. Sci. 118:845-850.

Ng, F. S. P. 1973. The fruits, seeds and seedlings of Malayan trees XII–XV. Malaysian For. 39:110-146.

Nichols, T. J. and A. A. Alm. 1983. Root development of container-reared, nursery-grown, and naturally regenerated pine seedlings. Can. J. For. Res. 13:239–245.

Nikolaeva, M. G. 1977. Factors affecting the seed dormancy pattern. p. 51-76. In: A. A. Khan (ed.), The physiology and biochemistry of seed dormancy and germination. North-Holland Publ. Co., Amsterdam.

Norman, E. M., K. Rice, and S. Cochran. 1992. Reproductive biology of Asimina parviflora (Annonaceae). Bul. Torrey Bot. Club 119:1-5.

Ourecky, D. K., and G. L. Slate. 1975. Evaluation system for papaw fruit. Northern Nut Growers Assoc. Ann. Rep. 65:57-58.

Owens, L. (publisher). 1994. Hatfield, Ky., W. Va. Battle for tourist dollars: Key happenings in the Hatfield-McCoy feud. Lexington Herald-Leader 9 Oct. 1994. Sect. B6.

Pascual, L., F. Perfectti, M. Gutierrez, and A. M. Vargas. 1993. Characterizing isozymes of Spanish cherimoya cultivars. HortScience 28:845-847.

Paull, R. E. 1982. Postharvest variation in composition of soursop (Annona muricata L.) fruit in relation to respiration and ethylene production. J. Am. Soc. Hort. Sci. 107:582-585.

Pena, J. E., A. Castineiras, R. Bartelt, and R. Duncan. 1999. Effect of pheromone for sap beetles (Coleoptera: Nitidulidae) on Annona spp. fruit set. Fla. Entomol. 82:475–480.

Peterson, R. N., J. P. Cherry, and J. G. Simmons. 1982. Composition of pawpaw (Asimina triloba) fruit. Northern Nut Growers Assoc. Ann. Rep. 73:97-107.

Peterson, R. N. 1986. Research on the pawpaw (Asimina triloba) at the University of Maryland. Northern Nut Growers Assoc. Ann. Rep. 77:73-78.

Peterson, R. N. 1991. Pawpaw (Asimina). Acta Hort. 290:567-600.

Peterson, R. N. 1997. How to hand-pollinate pawpaws. Fruit Gardener, Sept/Oct. p. 10–11. Peterson, R. N. 2003. Pawpaw variety development: a history and future prospects. Hort-Technology 13:449-454.

Picchioni, G. A., and C. J. Graham. 2001. Salinity, growth, and ion uptake selectivity of container-grown Crataegus opaca. Scientia Hort. 90:151-166.

Picchioni, G. A., C. J. Graham, and A. L. Ulery. 2004. Gypsum effects on growth and macroelement uptake of field-grown Asimina triloba (Pawpaw) irrigated with low-

saline, sodic water, HortScience 39(5):1104-1109. Picchioni, G. A., H. Karaca, L. Boyse, B. D. McCaslin, and E. A. Herrera. 2000. Salinity, boron, and irrigated pecan productivity along New Mexico's Rio Grande Basin. J. Env-

iron, Qual. 29:955-963.

Picchioni, G. A., S. Miyamoto, and J. B. Storey. 1990. Salt effects on growth and ion uptake of pistachio rootstocks. J. Amer. Soc. Hort. Sci. 115:647-653.

Pickering, C. 1879. p. 881. In: Chronological history of plants. Little, Brown, and Co., Boston. Pomper, K. W., D. R. Layne, and R. N. Peterson. 1999. The pawpaw regional variety trial. p. 353-357. In: J. Janick (ed.), Perspectives on new crops and new uses. ASHS Press, Alexandria, VA.

Pomper, K. W., S. C. Jones, and L. Barnes. 2000. The influence of low temperature storage on the germination rate of pawpaw [Asimina triloba (L.) Dunal]. Northern Nut Growers Assoc. Ann. Rep. 91:20-27.

Pomper, K. W., D. R. Layne, and S. C. Jones. 2002a. Incident irradiance and cupric hydroxide container treatment effects on early growth and development of container-grown pawpaw seedlings. J. Am. Soc. Hort. Sci. 127:13-19.

Pomper, K. W., D. R. Layne, S. C. Jones, and M. G. Kwantes. 2002b. Growth enhancement of container-grown pawpaw seedlings as influenced by media type, root-zone temperature, and fertilization regime. HortScience 37:329-333.

Pomper, K. W., D. R. Layne, and E. B. Reed. 2002c. Determination of the optimal rate of slow-release fertilizer for enhanced growth of pawpaw seedlings in containers. Hort-Technology 13:397-401.

Pomper, K. W., and R. J. Barney. 2003a. Introduction to the second international pawpaw conference. HortTechnology 13:410-411.

Pomper, K. W., S. B. Crabtree, S. P. Brown, S. C. Jones, T. M. Bonney, and D. R. Layne. 2003b. Assessment of genetic diversity of pawpaw varieties with inter-simple sequence repeat markers. J. Am. Soc. Hort. Sci. 128:521-525.

Pomper, K. W., D. R. Layne, and S. C. Jones. 2003c. Container production of pawpaw seedlings. HortTechnology 13:434-438.

Pomper, K. W., D. R. Layne, R. N. Peterson, and D. Wolfe. 2003d. The pawpaw regional variety trial: background and early data. HortTechnology 13:412-417.

Popenoe, W. (ed.). 1916. Where are the best papaws? J. Hered. 7:291-296.

Popenoe, W. (ed.). 1917. The best papaws. J. Hered. 8:21-33.

Postman, J. D., K. E. Hummer, and K. W. Pomper. 2003. Vascular disease in Oregon regional pawpaw variety trial. HortTechnology 13:418-420.

Ratnayake, S., J. K. Rupprecht, W. M. Potter, and J. L. McLaughlin. 1993. Evaluation of the pawpaw tree, Asimina triloba (Annonaceae), as a commercial source of the pesticidal annonaceous acetogenins. p. 644-648. In: J. Janick and J. E. Simon (eds.), New crops. Wiley, New York.

Reich, L. 1991. Uncommon fruits worthy of attention: a gardener's guide. Addison-Wesley,

Rizzini, C. T. 1973. Dormancy in seeds of Annona crassiflora Mart. J. Expt. Bot. 24:177-183. Rogstad, S. H., K. Wolff, and B. A. Schaal. 1991. Geographical variation in Asimina triloba Dunal (Annonaceae) revealed by the M13 "DNA fingerprinting" probe. Am. J. Bot. 78:1391-1396.

Shiota, H. 1991. Volatile components of pawpaw fruit (Asimina triloba Dunal). J. Agr. Food Chem. 39:1631-1635.

- Sohlheim, H., and L. Safranyik. 1997. Pathogenicity to sitka spruce of *Ceratocystis rubipenni* and *Leptographium abietinum*, blue-stain fungi associated with the spruce beetle. Can. I. For. Res. 27:1336–1341.
- Templeton, S. B., M. Marlette, K. W. Pomper, and S. C. Jones. 2003. Favorable taste ratings for several pawpaw products. HortTechnology 13:445–448.
- Thomson, P. H. 1974. The paw paw—brought up to date. p. 138–180. In: California Rare Fruit Growers Yearbook, Vol. 6. Calif. Rare Fruit Growers, Bonsall, CA.
- Vines, R. A. 1960. Trees, shrubs, and woody vines of the southwest. Univ. of Texas Press, Austin.
- Westwood, M. N. 1993. Temperate-zone pomology and culture, 3rd ed. Timber Press, Portland. OR.
- Wiese, T. D., and M. W. Duffrin. 2003. Effects of substituting pawpaw fruit puree for fat on the sensory properties of a plain shortened cake. HortTechnology 13:442–444.
- Wills, R. B. H., A. Poi, H. Greenfield, and C. J. Rigney. 1984. Postharvest changes in fruit composition of *Annona atemoya* during ripening and effects of storage temperature and ripening. HortScience 19:96–97.
- Willson, M. F., and D. W. Schemske. 1980. Pollinator limitation, fruit production, and floral display in pawpaw (*Asimina triloba*). Bul. Torrey Bot. Club 107:401–408.
- Wood, R., and S. Peterson. 1999. Lipids of the pawpaw fruit: *Asimina triloba*. Lipids 34:1099–1106.
- Young, D. R., and J. B. Yavitt. 1987. Differences in leaf structure, chlorophyll, and nutrients for the understory tree *Asimina triloba*. Am. J. Bot. 74:1487–1491.
- Young, J. A., and C. G. Young. 1992. Seeds of woody plants in North America. Dioscorides Press. Portland, OR.
- Zhao, G., J. H. Ng, J. F. Kozlowzki, D. L. Smith, and J. L. McLaughlin. 1994. Bullatin and bullanin: two novel, highly cytotoxic acetogenins from Asimina triloba. Heterocycles 38:1897–1908.
- Zimmerman, G. A. 1938. The papaw. Northern Nut Growers Assoc. Ann. Rep. 29:99–102. Zimmerman, G. A. 1941. Hybrids of the American pawpaw. J. Hered. 32:83–91.

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