Pawpaw (*Asimina*)

R. Neal Peterson[1]

"*Of all the important native fruits of the United States, the least known is probably the pawpaw*[2] [**Asimina triloba** (L.) Dunal], *which grows in the forests from the Gulf of Mexico to the Atlantic, west to Oklahoma and as far north as New York and Michigan. . Its creamy pulp is of exquisite texture in the mouth, while its distinctive flavor and its aroma, often too pungent, give it a decided individuality... The drawbacks of the fruit are largely of a commercial character. They are drawbacks which can probably be removed by intelligent breeding. With this idea a number of individuals have undertaken during the last few years to improve the pawpaw; but there is still plenty of room for work, and the American Genetics Association therefore feels the desirability of calling attention to the pawpaw, and pointing out the attractiveness of the problem it offers.*" That quote is dated 1916, from an article in the Journal of Heredity announcing a national contest for the best pawpaw. Today, three-quarters of a century later, that statement is equally true. The purpose of this chapter is to place in perspective the advances that have been made in pawpaw breeding, particularly since 1916, and to describe the germplasm that exists for creating further improvement of this delectable fruit.

History of domestication

Little is known about pawpaw selection before the 20th century, but a history of the pawpaw's early use by humans probably conforms to the evolutionary theory of plant domestication suggested by Rindos (1984). Rindos writes that "domestication is the result of coevolutionary interactions between humans and plants. . . [and] has three conceptually distinct phases mediated by different types of human behavior and occurring in distinct environments. Incidental domestication is the result of human dispersal and protection of wild plants in the general environment. Over time this relationship will select for morphological changes in the plants, preadapting them for further domestication. Specialized domestication is mediated by the environmental

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[2] The author observes the convention recommended by Thomson (1974) of using the spelling *pawpaw*. *Pawpaw* and *Paw Paw* are the universal vernacular spellings encountered in place names in the U.S. The alternate spelling of *papaw*, though common in the literature from 1900 to 1950, tends to be confused with *Carica papaya*, which is commonly called (and spelled) *papaw*.

impact of humans, especially in the local areas where they reside. The most important outcome of specialized domestication is the development of a unique ecological niche – the agroecology. Agricultural domestication, the culmination of the other two processes, involves the further evolution of plants in response to the conditions existing with the agroecology... [and] is roughly equivalent to what has simply been termed domestication in the literature of agricultural origins."

Dispersal of the Pawpaw

Many agents have been suggested as being dispersers of the pawpaw, but most are of doubtful importance. Opossum, raccoon, fox, squirrel, skunk, groundhog and turtles have been implicated by Little (1905), Van Dresel[3] (1938), and Glaser (1961) but seem too small to swallow the seed dependably. Water transport has been suggested by Bowden and Miller (1951) on account of the seed's buoyancy, but transport by water could play only a minor role[4]. It appears that humans have been the primary disperser of the pawpaw. *Asimina triloba*, however, is indigenous to North America, predating the presence of *Homo sapiens* by tens of thousands of years. Identifiable fossils closely resembling *A. triloba* date to the Late Miocene from New Jersey, and fossil fruits of *Asimina* have been recovered from the Eocene in Mississippi (Berry, 1916). Janzen and Martin (1982), pondering the mystery of the many Central American fruits that seem to lack coevolved fruit feeders, hypothesize that they were originally dispersed by the large mammals of the Americas that died out at the end of the Pleistocene (e.g., extinct equids, gomphotheres [which were mastodon-like proboscidians], ground sloths, glyptodonts). They conclude that North American fruits such as the pawpaw, persimmon, and osage orange also fit their hypothesis.

Incidental domestication.
The demise of the mastodons and other frugivorous giants of North America at the end of the Pleistocene might have consigned *Asimina triloba* to an evolutionary backwater of population decline, inbreeding, and genetic loss. The arrival of humans in North America toward the end of the Pleistocene probably saved *A. triloba* from such a fateful decline. The spread of pawpaws out of their southern Ice Age refugia into the once glaciated regions north of the Ohio River must have been accomplished primarily by humans. Native Americans expanded the ranges of some other native species which were useful as food and medicine, such as may apple (*Podophyllum peltatum*) pond nuts (*Nelumbo lutea*), Kentucky coffee tree (*Gymnocladus dioica*), and possibly American chestnut (*Castanea dentata*) (Yarnell, 1964). Given the pawpaw's value as a source of food, fiber and medicine (Millspaugh, 1887; Meijer, 1974; Allard, 1955; Krochmal and Krochmal, 1973), it is reasonable to believe that the early

[3] Opossum and gray fox may be dispersers; Van Dresel reported that stomach records of those two species contain pawpaw, although he did not state whether that was flesh, seed, or skin.
[4] Water will not transport seed above flood levels, however, and pawpaw seed loses its buoyancy as it imbibes water during stratification [unpublished observation].

inhabitants of eastern North America extended the range of the pawpaw, probably to the limits of its hardiness in the north and the limits of its drought tolerance in the west. In spreading the pawpaw, they would have acted as incidental domesticators, and may have exerted some selection in the direction of superior fruit quality.

Specialized domestication.

Early North Americans made the first improvements in the pawpaw, by selecting intentionally or nonintentionally superior fruiting characteristics, and thereby established the genetic base upon which modern advances have been made. In the process of clearing forest for field agriculture, native North Americans preserved valuable trees, including pawpaw (Yarnell, pers comm.). In of itself, preservation would not modify gene frequencies. However, preservation and protection in combination with the harvest of pawpaw bark for fiber could have exercised selection. The harvest of pawpaw fiber entails stripping the inner bark from the trunk of the tree, thereby killing the tree above ground, and stimulating the roots to recover by suckering. The entire plant may not die, but it is greatly weakened and is susceptible to infection If men and women harvested bark extensively, frequently, and in discriminating fashion, sparing those threes whose fruit or yield was superior, then the harvest of pawpaw fiher could have imposed considerable pressure towards the selection of superior fruiting characteristics. Regression analysis of pawpaw seed dimensions from seeds recovered in archeological digs shows no evidence of fruit selection (Richard Ford, pers. comm.); however, many fruit and yield characteristics will not be correlated with seed dimensions, and the question remains unresolved.

The preponderance of evidence suggests that if pawpaw selection occurred as part (or consequence) of cultural activity hy native Americans, then it was accomplished bv peoples who lived in the vallevs of the lower Ohio River and its major tributaries. It is from that region of the Midwest that the majority of pawpaw cultivars have originated. Other areas that gave rise to numbers of cultivars are Arkansas and eastern Kansas-western Missouri. There are, of course, alternative plausible explanations for the Midwestern U.S.A. origin of pawpaw cultivars It may be an artifact of non-random exploration and reporting; in the period 186C to 1960, the years during which most cultivars were selected, the Midwest was more literate, better educated, more active in national organizations, and more interested in scientific agriculture than was the South.

Towards agricultural domestication.

At the time of European contact, the native American societies of what is now the southeastern U S.A. were large, with well-developed agricultures and permanent fortified settlements and religious complexes. In 1541, the De Soto expedition traversed the region from Florida, the Carolinas, west to the Mississippi River, and encountered pawpaws being grown by the native peoples throughout much of the region (Pickering, 1879). English colonization of eastern North America and the westward expansion of the young United States was initially a setback for the incipient domestication of the pawpaw. Many stands of pawpaw were destroyed in the process of clearing the forests for agriculture as the best pawpaw groves were found growing on the same fertile, well-drained, alluvial soils that were best suited to row crops (Sargent, 1890). By the 18th and 19th centuries, however, the pawpaw had become an established item of rural American life, figuring in poem, song, game and geographical place names (Thomson, 1974; Kluger, 1984). The pawpaw helped sustain settlers in time of harvest failure (Little, 1905), and fed the Lewis & Clark expedition in western Missouri in the fall of 1810 when their rations ran low on the return trip east (Kluger, 1984).

Around 1900 interest in the pawpaw increased. A few pawpaw orchards were established, one in Danville, Indiana (in 1895 by James Little) and another in Charleston, West Virginia (ca 1910) (Amer. Genet. Assn., 1917). A national contest was held for the best pawpaws in 1916 as a means of calling attention to the pawpaw and of discovering superior pawpaw selections. The contest resulted in the identification of 7 superior new clones and of 14 already existing cultivars, and stimulated interest in the pawpaw (Amer. Genet. Assn., 1917). From 1917 to 1950 an additional 17 cultivars were selected and propagated, and large collections were built through seed and scion exchange by Buckman, Zimmerman, Hershey, and the Blandy Experimental Farm, in cooperation with numerous individuals whose names will never by known. During that period, breeding began on a small scale by Fairchild and Zimmerman (Flory, 1958). Since 1950, collections have been built by Davis, Hickman, Thatcher, Mansell, Peterson and others. The requirements of germination and seedling establishment were explicated by Little (1905), the U.S. Forest Service (1948), and Hershey (1957). The problems of transplantation were largely solved by Glaser (1961) and Hershey (1957). Successful methods of grafting and budding were reported by Davis (1974), Thomson (1974), and Hickman (1980). Selection indices has been proposed (Thomson, 1974; Ourecky and Slate, 1975). In 1974 Thomson brought together much of the original literature and published them in an anthology, including original solicitations from pawpaw growers.

Pawpaw biology has been a matter of continuing interest, resulting in a variety of studies. Insect pollinators, pollination biology, and fruit set were observed and informally studied by Zimmerman (1938, 1940), McDaniel (1958), Kral (1960), Bartholomew (1962) and Davis (1974). More thorough studies of pollination and reproduction were performed by Willson and Schemske (1980), Lagrange and Elliot (1985), and Ambrose and Kevan (1990). Hybridization experiments between *A. triloba* and other *Asimina* species were performed by Zimmerman (1938, 1940), McDaniel (1970), and Swartz (Peterson, 1986). The nutritional composition of the fruit was studied by Langworthy and Holmes (1917) and by Peterson et al. (1982), while seed composition was studied by Matsui (1981). Observations on the occasional phenomenon of pawpaw toxicity were recorded by Barber (1905). Taxonomic studies of the genus, based on field observation of habit and ecology, were made by Small (1933), Uphopf (1933), and Kral (1960). Lampton studied the developmental morphology of the ovule and seed (1952, 1957), and experimented with endosperm tissue culture (1952). Mohana Rao (1982) studied the fruit and seed anatomy.

Agricultural domestication.

Scientists at several universities are conducting experiments with pawpaw. James Flore of Michigan State University is investigating cultural requirements. At University of Maryland, Harry Swartz is experimenting with tissue culture, James Marshall is experimenting with food processing, and Carol Karahadian and Marilyn McGrath are analyzing volatiles. The author and Swartz are breeding and selecting pawpaw, in an effort to develop commercial quality cultivars. Since 1981 they have assembled a germplasm collection of roughly 1200 accessions, open-pollinated seedlings from the historic collections of Buckman, Zimmerman, Hershey, Allard, the Blandy Experimental Farm, plus some from modern cultivars (Peterson, 1986). The trees will be evaluated for three fruiting seasons, 1988 through 1990, followed by selection and controlled crosses. Three cycles of evaluation, selection and crossing (about 30 years) are anticipated in order to ensure the discovery of a variety of truly superior genotypes. A few cultivars may be identified in the first or second cycle. The following traits are critical needs in their breeding program, whose relative weights are as yet unassigned:

Fruit characteristics.

Moderate to large fruit size, 200-400 gm.

Attractive, clear skin colors with little blotching and streaking.
Thicker, tougher skin, affording greater protection.
Mild and agreeable aroma.
Mild to rich satisfying flavor, with a pleasant aftertaste.
Firm, custardy, melting flesh.
Few seeds of small size, with seed: fruit ratios less than 4 percent.
Good to excellent nutritive value.
Fruit that abscises early, at a firm-ripe stage.
Reduced metabolism, less perishable fruit.
Lower linolenic acid levels (reduced susceptibility to rancidity).

Tree characteristics.

Small tree size for easier harvest, less than 3 m.

Precocious bearing, 4 years or less.
Vigorous growth under low to medium inputs.
Open branching structure with strong crotch angles, self-pruning.
Fruit borne near the base of the branches for strong support.
High flower density, 3 or more flower buds per branch.
High fruit set under natural pollination, greater than 25 percent.
Consistently high yields, over 2 kg per meter of tree height.
Resistance to *Talponia plummeriana* Busck (pawpaw peduncle borer).
Cold hardiness and drought tolerance.

Propagation characteristics.

Rapid germination, in less than 60 days and greater than 80 percent.

Successful meristem tissue culture and rooting of plantlets.
Seedlings and young plants tolerant of exposure to direct sunlight.

Genetic base

Cultivars

Unlike many new crops which have little history of domestication, the history of pawpaw selection is relatively long and has resulted in many cultivars. Since 1900, at least 56 selections of pawpaw have been named and propagated (Table 1). With a few exceptions, all of these cultivars were selected from the wild, and most have been recorded in the literature. Unfortunately, 36 of these, dating mostly from before 1940, appear lost; they have either disappeared from cultivation, or have through the neglect and abandonment of collections lost the labels and records needed for proper identification (Peterson, 1986). The 20 extant cultivars date primarily since World War II, several of which have not been heretofore recorded.

Cultivars do not appear to have been selected outside the U.S.A., although *Asimina triloba* has been introduced to many temperate countries of both the northern and southern hemispheres. Pawpaw was introduced to England in 1736 by Peter Collinson (Dillwyn, 1843). Not long after that it was introduced to the continent of Europe. It was introduced to Japan around 1895; and again to the Kyoto agricultural experiment station in 1905 (Uehara, 1954). It has been introduced to the U.S.S.R., Argentina, Chile, India, Australia, and New Zealand at unknown dates (probably prior to 1950). The author has sent seed to agricultural experiment stations in Romania (1986), Argentina (INTA, San Pedro, 1985), and India (Tamil Nadu Agricultural University, 1983) and to private individuals in Italy (1985) and Nepal (1989). Swartz sent seed to Dr. Jordan of Catholic University, Santiago, Chile (1988).

By comparison with commercial fruit crops, the cultivars of the pawpaw are undescribed. The few published descriptions which exist report in general narrative style the circumstances of discovery, the appearance, flavor, and size of the fruit, and the month of harvest. They are short on specific details and exhibit no consistent standard of description. Omitted are quantitative measurements of the means and variation of yield, fruit size, seed size, and seed:fruit ratios that might permit comparison of cultivars, analysis of varietal response to different climates and cultural regimes, or analysis of inheritance and heritability of traits. Description of characters, such as size, proportion, color, etc. of leaf, bud, flower, fruit, seed, isozymes, etc. that could be used to differentiate and identify cultivars has not been attempted.

Table 1. Pawpaw cultivars[1].

Cultivar	Selected	Selector	Origin	Reference	Collection[2]
Lost or extinct					
Uncle Tom	1896	J.A. Little	Cartersburg, IN	Little (1905)	bb
Cheely	c. 1900	J. Cheeley	Iuka, IL	Buckman (1917)	bb
Hahn	c. 1900		Arkansas	Buckman (1917)	bb
Early Best	c. 1900	W.C. Stout	Indiana	Buckman (1917)	bb
Arkansas Beauty	c. 1900		Arkansas	Buckman (1917)	bb
Scott	c. 1900	C.S. Scott	West Virginia	Buckman (1917)	bb
Endicott	c. 1900	G. Endicott	Villa Ridge, IL	Buckman (1917)	bb
Hopes August	c. 1900	A. Hope	Paint, OH	Buckman (1917)	bb gaz
Hopes September	c. 1900	A. Hope	Paint, OH	Buckman (1917)	bb
Cox Favorite	c. 1900			Buckman (1917)	bb
Early Cluster	c. 1900			Buckman (1917)	bb
Propst Early	c. 1900			Buckman (1917)	bb
Ketter	c. 1900	Mrs. F. Ketter	Ironton, OH	Am.Gen.Ass. (1917)	jh gaz
Cheatwood	c. 1900	J. Cheatwood	Gallia, OH	Am.Gen.Ass. (1917)	
Martin	c. 1900	S.C. Martin	Springfield, OH	Am.Gen.Ass. (1917)	gaz
Rees	c. 1900	W. Rees	Pleasanton, KS	Am.Gen.Ass. (1917)	jh
Oswald	c. 1900	E. Oswald	Hagerstown, MD	Am.Gen.Ass. (1917)	
Potter	c. 1900	B.S. Potter	Julietta, IN	Am.Gen.Ass. (1917)	
Roach	c. 1900	J.C. Roach	De Kalb, MO	Am.Gen.Ass. (1917)	
Fairchild	c. 1925	D. Fairchild	'Ketter' seed	Zimmerman (1938)	gaz jh
Long John	c. 1930	B. Buckman'		Zimmerman (1938)	gaz jh
Taylor	c. 1930			Zimmerman (1938)	gaz jh
Tiedke	c. 1930			Zimmerman (1938)	gaz jh
Shannondale	c. 1930			Zimmerman (1938)	gaz jh
Osbourne	c. 1930			Zimmerman (1938)	gaz jh
Buckman	c. 1930	B. Buckman		Zimmerman (1938)	gaz jh
Schriber	c. 1930			Zimmerman (1938)	gaz jh

Table 1. Continued

Cultivar	Selected	Selector	Origin	Reference	Collection[2]
Holtwood	c. 1938	W. Hoopes[3]		Zimmerman (1940)	gaz jh
Hengst	c. 1938			Zimmerman (1940)	gaz jh
Gable	c. 1940	J. Gable[3]	Pennsylvania,	Zimmerman (1941)	gaz jh
Jumbo	c. 1940			Zimmerman (1941)	gaz jh
Betty Wirt	c. 1960		Wirt Co., WV	Bartholomew (1962)	
Mudge	c. 1960			Pape (1965)	
Lawvere	c. 1960			Pape (1965)	
Kercheval	c. 1960			Pape (1965)	
Extant					
Middletown	1915	E.J. Downing	Middletown, OH	E.J. Downing[4]	dff
Sweet Alice	1934	H. Jacobs	s. Ohio or WV	Holden Arboretum[4]	nnga nafex ha
Mason/WLW	1938	E.J. Downing	Mason, OH	E.J. Downing[4]	dff
G-2	1942	J.W. McKay	Zimmerman seed	J.W. McKay (1975)	jwm ct
M-1	1948	J.W. McKay	'G-2' seed	J.W. McKay (1975)	jwm ct
Overleese	c. 1950	W.B. Ward	Rushville, IN	Pape (1965)	nnga nafex
Glaser		P. Glaser	Evansville, IN	Thomson (1974)	nnga nafex
Little Rosie		P. Glaser	Evansville, IN	Thomson (1974)	nnga nafex
Silver Creek		K. Schubert		Thomson (1974)	nnga nafex ha
Zimmerman		G. Slate	Zimmerman seed	J.H. Gordon[4]	lhm
Davis	c. 1965	C. Davis	Illinois (?)	Davis (1969)	nnga nafex
Taylor	1968	C. Davis	Ingham Co., MI	Davis (1969)	nnga nafex
Taytwo	1968	C. Davis	Ingham Co., MI	Davis (1969)	nnga nafex
Mary Foos Johnson		M. Gibson		R.L. Ticknor[4]	osu
Sunflower	c. 1970	M. Gibson	s.e. Kansas	Davis (1975)	nnga nafex
Mango	c. 1970	M.C. Collins	Midwest (?)	M.C. Collins[4]	nnga nafex
Rebeccas Gold	1974	J.M. Riley	seed from C. Davis	J.M. Riley[4]	jmr crfg
Mitchell	1979	J.W. Hickman	Franklin Co., IL	Hickman (1980)	nnga nafex

Table 1. Continued

Cultivar	Selected	Selector	Origin	Reference	Collection[2]
NC-1	c. 1985	R.D. Campbell	'Davis'x'Overleese'	J.H. Gordon[4]	nnga nafex
Wilson	1985	J.V. Creech	Cumberland, KY	J.W. Hickman[4]	nnga nafex
Unnamed					
57+ clones	1979	O.E. White	Boyce, VA	Peterson (1986)	bef umd
50+ clones	1980	G.A. Zimmerman	Piketown, PA	Peterson (1986)	gaz umd
3+ clones	1981	H.A. Allard	Arlington, VA	Peterson (1986)	haa umd
12+ clones	1983	J. Hershey	Downingtown, PA	Peterson (1986)	jh umd
10+ clones	1984	B. Buckman	Farmingdale, IL	Peterson (1986)	bb umd

[1] Blanks denote unavailable information.

[2] bb = Benjamin Buckman, Farmingdale, IL.
gaz = George A. Zimmerman, Piketown, PA.
jh = John Hershey, Downington, PA.
dff = Downing Fruit Farms, New Madison, OH
nnga = the Northern Nut Growers Assn.
nafex = the North American Fruit Explorers
ha = Holden Arboretum, Mentor, OH.
jwm = John W. Mckay, College Park, MD.
ct = Charles Thatcher, Clairton, PA.
lhm = L.H. McDaniels, Ithaca, NY.
osu = Oregon State University, Aurora, OR.
jmr = John M. Riley, Santa Clara, CA
crfg = the California Rare Fruit Growers Assn
bef = Blandy Experimental Farm, Boyce, VA.

[3] According to Vines (1960)

[4] Personal communication.

Table 2. Composition of pawpaw, compared to peach and apple.

Constituent	Pawpaw[1]			Peach[2]	Apple[2]
	Maximum	Minimum	Mean	Mean	Mean
Proximates[3]					
Water	77.0	69.5	75.3	87.7	83.9
Fat	1.4	0.6	1.2	0.1	0.4
Protein	1.4	0.8	1.2	0.7	0.2
Carbohydrate	25.4	16.8	18.8	11.1	15.3
Fiber	3.5	1.4	2.6	0.6	0.8
Ash	0.6	0.7	0.7	0.5	0.3
Food energy	89[4]	77[4]	80[4]	43[4]	59[4]
Vitamins[5]					
A	105[6]	66[6]	87[6]	535[6]	53[6]
C	20.9	7.6	18.3	6.6	5.7
Thiamin	0.01	0.01	0.01	0.02	0.02
Riboflavin	0.09	0.09	0.09	0.04	0.01
Niacin	1.2	1.1	1.1	1.0	0.1
Minerals[5]					
Calcium	76	53	63	5	7
Potassium	368	314	345	197	115
Magnesium	120	109	113	7	5
Phosphorus	53	43	47	12	7
Iron	7.2	6.8	7.0	0.1	0.2
Zinc	0.9	0.9	0.9	0.1	0.0
Copper	0.6	0.4	0.5	0.1	0.0
Manganese	2.6	2.5	2.5	0.0	0.0
Fatty Acids[7]					
Palmitic	24.4	18.6	20.7	10.0	13.3
Palmitoleic	10.2	5.8	8.3	1.1	0.3
Oleic	38.0	23.3	31.5	37.8	3.9
Linoleic	9.0	8.1	8.5	48.9	24.2
Linolenic	24.4	16.9	19.5	1.1	5.0
Sugars[3]					
Sucrose	13.3	6.0	8.2	5.6	3.3
Fructose	2.8	1.3	2.6	1.3	7.6
Glucose	4.0	1.8	2.9	1.1	2.3
Essential amino acids[7]					
Isoleucine	6.8	4.7	5.8	2.9	4.2
Leucine	8.2	5.8	6.7	5.7	6.3
Lysine	6.3	4.2	5.0	3.3	6.3
Methionine	1.4	0.9	1.2	2.4	1.1
Cystine	0.6	0.2	0.4	0.9	1.6
Phenylalanine	4.9	3.7	4.3	3.1	2.6
Threonine	4.6	3.2	3.8	3.9	3.7
Tryptophan	0.9	0.4	0.8	0.3	1.1
Tyrosine	2.5	1.8	2.0	2.6	2.1
Valine	6.0	4.2	4.9	5.4	4.7

Economic Importance

Commercial sales of the fruit.

Pawpaws occasionally find their way to market. In Charleston, Parkersburg, and some other West Virginia cities, pawpaws are sold in farmers markets for $1.39/kg ($.99/quart); sales are modest (Thomson, 1985). An infrequent outlet are organic food stores (Thomson, 1985). The Michigan Marketing Association supplied a few select restaurants in 1989 with 30-36 kg of pawpaws, at a delivered price of $11/kg (Christopher Steele, pers. comm.).

In all instances, the pawpaws for sale were gathered from the wild or from home grown trees. The author knows of no instance in the U.S.A. where pawpaws are cultivated in commercial orchard fashion, although he has received inquiries about its possibilities. In Italy, France, and Australia several growers have trial orchards (Giovanni Bubani, Domenico Montanari, Peter Taverna, pers. comm.). In 1988, James Flore, professor of horticulture at Michigan State University, discovered pawpaws being sold as papaya (!) in a grocery in London, England, for nearly $8/kg (pers. comm.). The origin of those fruits is unknown.

Home production and nursery sales.

The greatest consumption of pawpaws is from fruits gathered in the wild or from trees grown for personal use. The quantity of pawpaws consumed is unknown. However, the number of people growing pawpaws for home consumption seems to be steady and slowly growing, judging from the sales of mail-order pawpaw trees. Knowledgeable nurseries have begun to pay strict attention to the stringent transplant requirements of pawpaws, thereby assuring transplant success. F. W. Schumacher Co., a tree seed supply company, reports that "the prospects for pawpaw seed are very good; the industry as a whole is moving towards native plants, with a strong undercurrent of interest in edible plants." It is difficult to gauge overall industry demand. Schumacher is the largest supplier of pawpaw seed, with annual purchase around 50 kg at a price for improved seed of $26-33/kg. Assuming 750 seed per kg (representative of seed from the University of Maryland collection at Wye) and a 70% germination/survival rate, 50 kg of seed establishes a minimum national annual production of about 25,000 trees.

Nutritional importance.

The pawpaw has been shown to have high nutritional quality (Table 2), especially as compared to typical temperate fruits such as apple and peach (Peterson et al., 1982).

[1] Raw unpeeled fruit (Peterson et al., 1982).
[2] Raw unpeeled fruit (Gebhardt et al., 1982; Matthews et al., 1987).
[3] Gm/100 gm edible portion.
[4] Kcal/100 gm edible portion.
[5] Mg/100 gm edible portion.
[6] IU/100 gm edible portion.
[7] Percent composition of lipids and protein.

Particularly notable are its low moisture content, its high caloric content, and its high content of vitamins A and C, minerals P, Mg, S, Ca, and Fe, and the essential fatty acids linoleic and linolenic. It is also notable for a higher protein content and for an exceptionally favorable balance among the essential amino acids, having a chemical score of 45; the most limiting amino acid was methionine, which is usual for protein from plant sources other than cereals grains. Peterson et al. (1982) noted that despite the smallness of their sample, 27 fruits from 4 clones, the nutrient composition varied considerably among the clones, suggesting that the high nutritional value of the pawpaw could be further improved by plant breeding.

Problems of Genetic Significance

Commercial quality pawpaw cultivars do not exist. The 20 extant cultivars listed in Table 1 are well suited to home production, but none exhibit the combined excellence in flavor, aroma, texture, low seed: fruit ratios, aesthetics, yields, ease of propagation, and shipping storage ability needed for commercial cultivation. The following economically relevant traits of pawpaw have been listed roughly in order of descending importance as problems: yield, fruit set, harvest methods, seediness of the fruit, perishability, (storage and handling, prolonged juvenility, propagation difficulties, aesthetics/appearance, susceptibility to pests, toxic compounds/allergens, nutrient levels, flavor and texture, and fruit size variability. The first six traits encompass the greatest problems associated with pawpaws and so are treated in greater detail below. Propagation difficulties, susceptibility to pests, and the presence of toxic compounds are also detailed.

Yield.

Pawpaw yields are notoriously low, a trait they share in common with their tropical Annonaceae relatives, the *Annonas* (Thakur, 1965; Farooqi et al., 1970; Gazit et al., 1982). This problem is a potential obstacle to commercial development. It requires the selection of higher yielding types in order that yields may exceed the minimum needed for profitability as determined by the product price and the costs of production. Bartholomew (1962) reported the typical yield from one superior tree was 4 kg. In contrast, Ourecky and Slate (1975) reported that a yield of 11.5-23 kg from a mature tree was reasonably good, but obviously based their figure on Gould's (1939) report of .5 to 1 bushel yields, since the wording is the same and the quantities are equivalent. Little (1905) estimated that 1250-1500 trees may be planted to the hectare without crowding. Multiplying Little's figure by the Ourecky-Slate figure and assuming an inverse relationship between tree density and yield per tree generates a yield per hectare of 17,300 to 29,000 kg (9,700-11,700 kg/acre). Assuming a grower price between $1.10 and $3.30/kg, this yield equals $19,000 to $95,000 per hectare ($7,700-$38,700 per acre). (Since market prices for cultivated pawpaws do not exist, price for cherimoya (*Annona cherimola* Mill.), a close relative of pawpaw, was used here as a proxy pawpaw price. Frieda's Finest/Produce Specialties of Los Angeles reported (pers. comm.) that southern California cherimoya growers received $1.10 to

$3.30 per kg ($.50-$1.50/lb) in 1989.) Operating costs are unknown but should be relatively low; pawpaws require low levels of inputs, having excellent pest resistance and good drought tolerance[5].

Fruit set.
The major components of pawpaw yield are probably tree vigor, blossom density, and fruit set. Fruit set in pawpaw is determined primarily by pollination success, which depends on successful insect pollinator activity, pollen compatibility, and the normal development of the fruit (i.e., the absence of abortion). Of the components of fruit set, the problems of low yields are almost entirely related to the insufficient availability and abundance of pollinators (Willson and Schemske, 1980; Lagrange and Tramer, 1985) and to unsuccessful pollinations and/or fertilizations caused by pollen-incompatibility (Zimmerman, 1940; McDaniel, 1958). The low yields of the *Annonas* are likewise related to low rates of natural pollination, and in commercial practice are solved by hand-pollination (Thakur, 1965; Farooqi et al., 1970). Even in Israel, where labor is expensive, hand pollination is sometimes resorted to (Gazit et al., 1982).

Inadequate pollination can result from problems of the biology and ecology of the pollinators. Flies (Muscidae and Sarcophagidae) and beetles are believed to be the primary pollinators (Pammel, 1903; Kral, 1960; Davis, 1974; Willson and Schemske, 1980). Low levels of pollinator activity may be caused by inclement weather, predator interference, low nectar production, or the unattractiveness of the flowers. This area has not been studied. Nothing is known about the abnormalities that may occur in the course of embryo, seed, and fruit development in pawpaw that may cause fruit to abort. In the orchard setting at Wye, Maryland, U.S.A., pollination has not been a problem, fruit set has been abundant, and fruit abortion has been common (10-20%) in the first month. In the wild, where large groves may be composed of a single or a few clones, pollen-incompatibility can be a primary source of low yields. The pawpaw is an obligate outcrossing species, although there are occasional reports of self-compatible clones (Davis, 1974; Robinson, 1974).

Harvest difficulties.
Maintaining quality in the process of harvest is a problem, because pawpaws are soft and easily bruised. Fruits are difficult to see beneath the dense foliage, and being green in color are easily missed. Color change does not signal ripening of the fruit; ripeness is judged by softness and aroma. Because pawpaw trees normally grow 5 to 7 m high, some device will be required for picking higher fruits, but ladders seem unsuitable because of the weakness and flexibility of the tree.

Seediness of the fruit.
Judging from the comments of many who have tried fresh pawpaw, the quantity of

[5] Observation of the Wye collection in the drought of 1988. We attribute this resistance to the deep taproot.

seed relative to the quantity of flesh is a major drawback. Manual preparation of the fruit for use in recipes also indicates that a high proportion of seeds is a problem. These were two of three problems mentioned by Frieda's Finest/Produce Specialties in their evaluation of unimproved pawpaws (pers. comm.).

Perishability.

The major reason given by the American Genetics Association in their contest announcement of 1916 for the failure of the pawpaw to be commercially marketed was the perishability of the fruit. This was also the major problem identified by Frieda's Finest/Produce Specialties. Perishability is a function of the fruits physiology and metabolism. Wardlaw and Leonard (1936) identified *Asimina triloba* as a climateric fruit. Abeles (unpublished, 1983) found that underripe fruit may be stored for 14 days at 5° C without damage, and may then be brought to room temperature where it will proceed to ripen in 6 to 8 days. The fully ripe fruit remained edible for only 3 days at room temperature. At the peak of respiration, the fruit was observed to evolve ethylene at a rate of 40 microliters/kg/hr and carbon dioxide at a rate of nearly 200 microliters/kg/hr. Controlled atmospheric storage methods and semi-permeable plastic films have not been tried.

Storage and handling.

The pawpaw's flesh is soft and custardy and the skin is thin; thus the ripe fruit is easily bruised. To further complicate matters, mechanical bruising often leads to the formation of off-flavors after a day or two (although not invariably, depending on the clone). Although the presence of the large seeds diminishes bruising to an extent by contributing some mechanical strength to the fruit interior, this attribute is of little importance in the best fruits which have a very low percentage of seed. Some clones of pawpaw have a thicker, more leathery skin which offers some protection (Amer. Genet. Assn., 1917), but none approach the hard rind of certain varieties of the cherimoya.

Germination.

The pawpaw propagates by means of seeds, rootsuckers, and possibly rhizomes. Germination is not inherently difficult. The major inconvenience is the slowness of germination which is imposed by seed dormancy combined with embryo immaturity. In storage the seed must not be allowed to dry out, and must be stratified (0-5° C) for 90-120 days (USDA-Forest Service, 1948), the length of period probably depending on the latitude of the accession. Germination is best in a well-drained, well-aerated soil with pH 5.5-7.0, and in temperatures fluctuating diurnally between 25° and 30° C. The author (unpublished) found on average, using seed from a variety of sources, that seed geminated most quickly and the radicle elongated most rapidly at 30° C, with the radicle emerging in 18 days (±6), the primary root growing to about 35 cm, and the epicotyl emerging on day 64 (±8). Germination is hypogeal and the plumule is extremely sensitive to direct sunlight, being easily killed by one day's exposure (Little, 1905; Hershey, 1957; Davis, 1974; Thomson, 1974). This sensitivity to direct sunlight remains in the young plant for one or two years. Since seedlings germinated and grown under glass do not exhibit this sensitivity, lethality is presumably caused by UV radiation. In the field, pawpaw seeds normally germinate from mid-July to mid-August, and grow very little the first year (5-10 cm). Experiments have shown that long daylengths typical of early summer are most conducive to growth (Allard, 1955). In the greenhouse, seed planted February 1 germinated April 1 (roughly) and grew 25-50 cm the first year, whereas seed planted 6 weeks earlier germinated during the short days of February, grew about 10 cm, and then set a terminal bud (Peterson, unpublished).

Asexual propagation.
Despite the versatility and facility with which a variety of grafting and budding techniques may be used on the pawpaw (Davis, 1974; Thomson, 1974; Hickman, 1980), grafting as a method of multiplying pawpaw cultivars has a major drawback: root-suckers inevitably sprout some distance from the main trunk, reproducing the root-stock genotype, not the cultivar. Methods which would circumvent this problem, namely asexual propagation by tissue culture or vegetative cuttings, have not been discovered. Root cuttings have given variable results that depend on the clone (Thomson, 1974) and the time of year the cuttings are taken (Glaser, 1961). Hardwood cuttings fail almost 100 percent of the time (Thomson, 1974). Tissue culture methods are being investigated but results have not yet been reported (Hickman, 1987).

Pest resistance.
Although the pawpaw is frequently extolled for being free of pests, that is not entirely true. The most horticulturally important predator is the larval stage of a small Tortricid moth, *Talponia plummeriana* Busck (Heinrich, 1926; MacKay, 1959), christened by Swartz "the pawpaw peduncle borer." This pest, about 2-5 mm long, burrows in the soft tissues of the receptacle beneath the ovaries, causing the flower to wither, blacken, and drop, and can be the cause of a large loss of flowers in some years (Allard, 1955).

Another pest of potential economic consequence is the larva of *Eurytides marcellus* Cramer (syn. *Papillio marcellus*), the Zebra Swallowtail butterfly. These larvae are exclusive feeders of young *Asimina* foliage. Damman (1986) studied the Florida species of *Asimina* and found that all were preyed upon by *E. marcellus*, but that the woolly-leafed pawpaw, *A. incana* (Bartr.) Exell, resisted attack better because of a heavy leaf pubescence, and that under normal circumstances *E. marcellus* larvae were heavily parasitized and were aggressively cannibalistic. Damage caused by *E. marcellus* in the collection at Wye, Maryland, U.S.A., has been generally light; small, newly transplanted pawpaws can be defoliated, however. Micro-organisms do not appear to be of economic consequence. Late in the growing season a leaf spot condition is common that can be caused by a variety of fungi, principally *Mycocentrospora asiminae* (Ellis et Kellerm.) Deighton, *Rhopaloconidium asiminae*, (Ellis et Morg.) Petr. and *Phyllosticta asiminae* Ellis et Kellerm. (Farr et al., 1989); occasionally the skin of the fruit may be infected (species unidentified); neither condition has been found to be a problem.

Illness due to pawpaw.
Some individuals react badly to eating the fruit, developing skin rash, nausea, vomiting or diarrhea. *In some cases an allergy exists to something in the leaves of the tree* and in the skin of the fruit (Buckman, 1917). Barber (1905) investigated instances of pawpaw poisoning and concluded that a special predisposition on the part of the person was necessary; that severe poisoning was rare; that milder poisoning may often be attributed to some other plant; and that fully ripened fruits were less likely to be harmful. The various tissues of the tree (especially bark, leaves, and seeds) are known to contain a great variety of protective compounds: alkaloids, phenolic acids, proanthocyanidins, tannins, flavonoids, and acetogenins (Leboucf et al., 1982; Rupprecht et al., 1986). It is not known what compounds in the fruit cause adverse reactions; they are thought to be concentrated in the skin. Infrequently (<1%) seeds may fail to develop normally, leaving exposed endosperm. As the endosperm is high in alkaloids and highly toxic to mammals (Matsui, 1981), accidental ingestion of compounds from exposed endosperm could lead to poisoning.

Genetic diversity

Taxonomy

Asimina triloba (L.) Dunal is a member of the family Annonaceae, which is included within the order Magnoliales, the most archaic of the orders of the class Magnoliopsida (i.e., dicotyledons) (Cronquist, 1981). Although it shares many primitive features with the Magnoliaceae and other families in the order (namely flowers with indefinite number of free floral parts, spirally arranged stamens, free carpels, etc.) the Annonaceae are considerably more advanced than the other families. They are a highly successful and diversified evolutionary lineage with about 130 genera and about 23,000 species, which are almost wholly confined to the tropics and to low elevations (Cronquist, 1981).

Leboeuf et al. (1982) note that the genera of Annonaceae are notoriously difficult to divide into natural groupings. Fries (1939), in a major revision of Annonaceae, assigned *Asimina* to the tribe Uvarieae of the subfamily Annonaideae. Hutchinson (1964), however, assigns the genus to the hexapetalate genera of the subtribe Xylopineae of the tribe Unoneae of the subfamily Annonaideae. The classification of *Asimina* has gone through numerous changes, before arriving at its present status as a well-established biological and nomenclatural unit (Kral, 1960). It was first included with *Annona* by Linnaeus in 1753, then assigned a separate genus *Asimina* by Adanson in 1763. It was transferred to *Porcelia* by Persoon in 1807, returned to *Asimina* by Dunal in 1817, transferred to *Uvaria* by Torrey and Gray in 1838, and returned again to *Asimina* by Gray in 1886. Small (1933) split it into 2 separate genera, *Asimina* and *Pityothamnus*, and in 1939 Fries merged them again into the one genus, *Asimina*.

Asimina is the only genus of the Annonaceae native to the temperate zone, with *A. triloba* being the hardiest species, growing as far north as the Great Lakes of North America (southern Michigan and southern Ontario). In earlier geologic times *Asimina* was more widely distributed than today; fossil leaves (*Asimina eocenica* Lesq.) have been recovered in Texas, Colorado, and Wyoming from the Eocene (Lamotte, 1952). In 1960, Kral published the most complete treatment of the genus, based upon extensive field work and thorough examination of herbarium specimens. He recognizes eight species as comprising *Asimina*: *A. triloba*, *A. parviflora* (Michx.) Dunal, *A. obovata* (Willd.) Nash, *A. incana*[6], *A. reticulata* Shuttlew. ex Chapman, *A. longifolia* Kral, *A. pygmaea* (Bartr.) Dunal, and *A. tetramera* Small. These eight have affinities that subdivide *Asimina* into essentially 2 groups, the northern pawpaws and the Florida dwarf pawpaws.

The northern pawpaws (*A. triloba* and *A. parviflora*.).
Asimina triloba is the common northern pawpaw, a small tree, to 11 m tall. It is the hardiest of the 8 species, to zone 5 (-25° C). Adapted to a humid continental climate, it requires a minimum of 400 annual chill units (based on Swartz and Gray, 1982), a minimum of 160 frost-free days or 1450 total growing degree days (calculated to a 10° C base with a 30° C maximum), and a minimum of 80 cm of precipitation annually with the majority during the spring and summer. It prefers rich, moist, well-drained soils. This is the most common and wide-spread species. Its range covers most of eastern North America, principally the interior where it is a minor but frequent component of the deciduous forest; it is seldom found near the coast. Principal pollinators are flies and beetles (species unidentified). Principal dispersers are thought to be humans, raccoons, and opossums. It is not as plentiful as 200 years ago, because of the clearing of forests for agriculture. Although valuable germplasm may have been lost, the species is in no danger.

Asimina parviflora is the small-flowered pawpaw or dwarf pawpaw. It is a tall shrub, to 6 m tall, that closely resembles *A. triloba*, except that it is smaller in all its characteristics and is less hardy, to zone 7 (-15° C). It is adapted to an ocean moderated climate of the southeastern and southern Coastal Plain and inland through the piedmont. It prefers rich moist soils but can also be found on dry uplands. Principal pollinators are probably beetles. Seed dispersers are believed to be turtles, raccoons, and opossums. As with *A. triloba*, *A. parviflora* is in little danger of being reduced by present human activity.

[6] Kral (1960) proposes that the proper name for the woolly-leaved pawpaw is *A. speciosa*. I depart from Kral in this instance, by following Wilbur (1970) who argues that the earlier *A. incana* is correct. Wilbur also notes that the correct spelling, about which there has been some confusion, is *incana* not *incarna*.

The Florida dwarf pawpaws (*A. incana, A. reticulata, A. longifolia, A. obovata, A. pygmaea,* and *A. tetramera*).
These are shrubs, which range in height from very small (0.3 m) to moderate (1.5 m) to tall (4 m). They are only marginally hardy, to zone 9 (-2° C), and are primarily adapted to sandy soils in the warm wet maritime climate of peninsular Florida. The ranges of *A. longifolia, A. incana,* and *A. pygmaea* extend somewhat further north, into southern Georgia and Alabama. Pollinators are principally beetles (Scarabeidae) (Norman and Clayton, 1986), possibly flies; pollinators are thought to vary according to flower color. Seed dispersers may be tortoises, raccoons, and opossums. In spite of being endemics with restricted ranges, they are mostly nonendangered. *Asimina incana* and *A. reticulata* are weedy, react favorably to human disturbance, and are increasing in number (Kral, 1960). *Asimina obovata,* although more restricted (north central Florida, particularly the Ocala National Forest) is apparently a stable population. *Asimina tetramera,* the species most restricted in habitat (old dune scrub vegetation along the east coast of south Florida) has been reduced to two or three sites where it numbers fewer than 200 stems (probably fewer clones since asexual propagation is common in *Asimina*). Ward (1982) lists it as an endangered species.

The manner of variability, similarity and divergence of traits between the 8 species is not such as leads to consistent species groupings. The flowering traits of color and odor and of flowering habit are the most disjunct and noncontinuous, and divide the species into 4 groups which reveal the differing degrees of affinity among them (Table 3). The descriptions in Table 3 are based on Kral's understanding of *Asimina* with only minor elaboration from the author's experience and collected data. For a more detailed description of the species, the reader should consult Kral (1960).

Genetic Variation

Within *Asimina* the genetic variation is considerable, as is seen in Table 3, with differences in habit, indumentum, leaves, flowering habit, flowers, fruits, seeds, hardiness, and site-soil preference. Specifically:

Habit ranges from that of a small tree, through intermediate sizes of shrubs, to the very small shrub. All species are reported to spread underground, via rootsuckers and/or rhizomes. Some are stoloniferous.

Indument of buds and young growth varies in density from heavy to sparse, and in color from whitish blonde through orange, red, and brown.

Leaves vary from 4 to 30 cm in length. Leaf texture varies from membranaceous to coriaceous. Leaf shape varies from obovate through oblong-oblanceolate to linear lanceolate. The edges of the leaves may be more or less revolute or not at all revolute. The leaf position varies from pendant to ascending secund.

Flowering habits are of three distinct types: (1) flowers arising from lateral buds in the axils of the previous year's growth, (2) flowers arising from lateral buds in the axils of the current year's growth, and (3) in *A. obovata,* flowers arising from buds terminating the shoot growth of the current year.

Flowers occur as essentially two distinct morphs with a minimum of intergrading between the two: smaller, nonshowy, maroon flowers with a fetid odor; and larger, showy (white, yellowish, or pink) flowers with a fragrant aroma.

Fruit varies in size from 4 gm to 400 gm. The flavor varies from sweet, aromatic and delicious to bitter, resinous and insipid. The skin ranges from thin and tender to rough, leathery, and nearly hard. The proportion of fruit which is seed varies from 4 percent to 45 percent.

Seeds vary from 1 to 2.5 cm in length, and from .2 to 2.0 gm in weight. The shape varies from oblong-flat to round; color varies from tan to chestnut to ebony; the surface varies from dull to lustrous.

The dwarf pawpaws exhibit considerable variation within each species. Fruit quality is not consistently poor. Although most are terrible, some are merely poor, and occasional clones have good flavor; for instance, the author tasted an *A. reticulata* fruit in 1980 whose flavor was typical of a good *A. triloba*. The seed:fruit ratio varies considerably, from a low of 11 percent to a high of 45 percent and a mean of 28 percent. The skins are usually tough and thick, even hard. Some clones of *A. obovata* have tender skin like *A. triloba*. *Asimina obovata* is also notable for having a variety of fruit skin tones; the green ground color, similar to *A. triloba*, is often overlaid with shades of lavender and coated with a dense waxy bloom. Other species have skins that are deep brown or black (*A. incana* and *A. longifolia*), or that are coated with a fine reddish pubescence (*A. incana* and *A. parviflora*).

Quantitative Variation

Few reports have discussed variation in *A. triloba* in the context of breeding (Little, 1905; Amer. Genet. Assn., 1917; Ourecky and Slate, 1975; McKay, 1975) and even fewer have presented quantitative data[7] (Peterson et al, 1982; Peterson, 1989). Since 1986, the author has taken measurements of tree growth, blossom count, cluster count and fruit count, individual fruit weight, seed weight, etc. from over 130 individual six-year old seedling trees in the collection at Wye, Maryland, U.S.A. Table 4 presents statistics from these data. Obviously, these data are not representative; the trees were in their first year of bearing; and furthermore, the Wye collection is a decidedly nonrandom sample of the *A. triloba* population. These data, however, being the first such available, tentatively provide a baseline for later studies assessing variation in horticulturally relevant traits, and begin to establish a context for judging the breeding potential of individual clones.

Of the 13 variables listed in Table 4, five appear normal, that is, distributed fairly symmetrically about their mean with relatively small coefficients of variation. These normal variables are height, growth rate, seed size, the number of seeds per fruit, and the seed:fruit ratio. The remaining 8 variables are highly skewed, i.e., distributed nonsymmetrically as shown by a great disparity between the maximum and mini-

[7] Langworthy and Holmes (1917) in their study of the food value of pawpaw analyzed the seed, skin, and pulp composition of a representative sample of ten fruits. In their sample, size ranged from 51 to 78 gm and the seed:fruit ratio ranged from 14.8 to 22.6 percent.

Table 3. Characteristics and relationships of the *Asimina* species.

FLOWERS DEVELOP ON GROWTH OF PREVIOUS YEAR

FLOWERS MAROON AND FETID

	A. triloba (L.) Dunal	*A. parviflora* (Michx.) Dunal
a.	Small tree, 1.5-11 m.	Tall shrub of 1-6 m.
b.	Dark brown.	Reddish brown or tan.
c.	Obovate to oblanceolate, acuminate to acute, 15-30 cm long, membraneceous.	Obovate to oblanceolate, acuminate to acute, 6-15 cm long, membraneceous.
d.	Axillary, 2-5 cm broad, outer petals 1.5-3 cm long.	Axillary, 7-15 mm broad, outer petals 1-1.3 cm long.
e.	5-15 cm long, 25-300 gm, with an 8-24% seed:fruit ratio.	3-7 cm long, 5-50 gm, with a 25-40% seed:fruit ratio.
f.	Poor to excellent.	Poor to insipid.
g.	1.5-2.5 cm long, .5-2 gm, castaneous.	1-1.5 cm long, .6-1.2 gm, castaneous.
h.	Rich hardwood forest, river bottoms.	Rich woods, coastal hammocks.
i.	Well-drained loam.	Alluvial or sandy.

FLOWERS WHITE AND FRAGRANT

	A. reticulata Chapm.	*A. incana* (Bartr.) Exell
a.	Copiously branched shrub, to 1.5 m tall.	Copiously branched shrub, to 1.5 m tall.
b.	Rusty or orange.	Whitish or yellow.
c.	Oblong to elliptic or cuneate, 5-8 cm long, coriaceous.	Obovate to ovoid or elliptic, 5-8 cm long, coriaceous, pubescent.
d.	Axillary, outer petals 3-7 cm long.	Axillary, outer petals 3-7 cm long.
e.	4-7 cm long, 5-25 gm, with a 10-45% seed:fruit ratio.	3-8 cm long, 5-40 gm, with a 15-35% seed:fruit ratio.
f.	Poor to good.	Poor to insipid.
g.	1-2 cm long, .2-.5 gm, dark to pale brown, lustrous.	1-2 cm long, .4-.7 gm, dark to pale brown, dull.
h.	Pine flatwoods, fields.	Pine flatwoods, sand hills, fields, scrub.
i.	Moist, poorly drained sands.	Well-drained sands.

LEGEND: a=habit, b=indumentum, c=leaves, d=flowers, e=fruit, f=flavor, g=seeds, h=site, i=soil.

FLOWERS DEVELOP ON GROWTH OF CURRENT YEAR

A. pygmaea (Bartr.) Dunal

a. Dwarf shrub, 20-30 cm tall.
b. Sparse, reddish.
c. Obovate to cuneate, or oblanceolate, 4-7 cm long, coriaceous, ascending.
d. Axillary, outer petals 1.5-3 cm long.
e. 3-4 cm long, 3-10 gm, with about 30% seed:fruit ratio.
f. Poor to insipid.
g. Approx. 1 cm long, .2 gm, brown, shiny.
h. Slash pine-palmetto flatwoods, old fields.
i. Sandy.

A. tetramera Small

a. Tall shrub of 1-3 m.
b. Sparse, reddish.
c. Oblanceolate to elliptic, 5-10 cm long, coriaceaous.
d. Axillary, 2.5-3 cm broad, outer petals 2-2.5 cm long.
e. 5-9 cm long (weight and seed:fruit ratio are undetermined).
f. Poor.
g. 1-2 cm long, (weight undetermined).
h. Ancient coastal dunes.
i. Sands.

A. longifolia Kral

a. Shrub, 1-1.5 m.
b. Sparse, pale
c. Linear-elliptic to linear-oblanceolate, 5-15 cm long, coriaceous, horizontal.
d. Axillary, outer petals 3-8 cm long.
e. 4-10 cm long, 5-50 gm, with a 15-30% seed:fruit ratio.
f. Poor.
g. 1-2 cm long, .4-.9 gm, dark brown, shiny.
h. Pine flatwoods, old fields, scrub.
i. Sandy.

A. obovata (Willd.) Nash

a. Shrub (rarely a small tree), 2-4 m tall.
b. Red.
c. Obovate to oblong, oblanceolate to ovate, 4-10 cm long, coriaceous, lustrous.
d. Terminal, outer petals 6-10 cm long.
e. 5-9 cm long, 10-70 gm, with a 15-45% seed:fruit ratio.
f. Poor to insipid.
g. 1-2 cm long, .4-1.5 gm, brown to castaneous.
h. Dry sand ridges, dunes.
i. Well-drained sands.

LEGEND: a=habit, b=indumentum, c=leaves, d=flowers, e=fruit, f=flavor, g=seeds, h=site, i=soil.

Table 4. Variation in *Asimina triloba* in the Wye collection, Maryland, U.S.A., 1988.

Trait	Mean	Maximum	Minimum	Z scores[1]		Standard deviation	C.O.V.	Sample size
				Max.	Min.			
Height(M)	1.37	2.74	0.30	3.2	-2.5	0.43	0.315	765[2]
Total fruit (#)	13.1	70.0	3.0	5.7	-1.0	9.9	0.755	130[3]
Total yield (kg)	1.04	4.42	0.17	4.2	-1.1	0.81	0.778	130
Growth rate (m/yr)	0.40	0.91	0.01	2.7	-2.1	0.19	0.474	765
Blossom density (#/m height)	17.8	124.2	2.2	6.5	-1.0	16.3	0.916	185[4]
Fruit set[5] (%)	19.5	66.7	1.2	3.6	-1.4	13.0	0.667	185
Fruit density (#/m)	7.9	31.9	1.6	4.4	-1.1	5.5	0.698	130
Yield density (kg/m)	0.62	2.08	0.10	4.9	-1.3	0.41	0.793	130
Cluster size (#, av.)	2.2	6.0	1.0	4.2	-1.4	0.9	0.409	185
Fruit size (gm)	82.4	235.6	32.1	5.3	-1.7	29.1	0.353	130
Seeds per fruit (#)	8.3	12.6	4.6	2.6	-2.3	1.6	0.196	130
Seed-fruit ratio (.01 gm/gm)	9.2	17.8	3.4	3.2	-2.2	2.6	0.287	130
Seed size (gm)	0.87	1.44	0.25	2.6	-2.9	0.22	0.250	130

[1] Standardized values: the deviation from the mean divided by the standard deviation.
[2] Includes all *A. triloba* in the nursery.
[3] Excludes all trees with fewer than four fruits
[4] Excludes all trees with fewer than four flowers.
[5] The number of clusters formed per 100 blossoms.

mum values of the Z scores (standardized values), and by a large coefficient of variation. These skewed variables are total number of fruit, total yield, blossom density, fruit set, fruit density, yield density, cluster size, and fruit size. The skewness of the pawpaw population in the Wye collection towards floriferousness, higher fruit set larger fruit, and greater yields reflects the origins of our accessions from the historic collections of cultivars. It is particularly significant that blossom and yield traits are so highly skewed, as pawpaw is notorious for low yields, a major obstacle to commercial production.

Genetic solutions

Many, if not all, of the problems outlined in the earlier section have potential genetic solutions within the gene pools of *Asimina triloba* and the other *Asimina* species. Those other species are relevant because the transfer of traits from them to *A. triloba* has been proven realistic and practical. Kral (1960) reports 6 different hybrid combinations of the Florida dwarf pawpaw species (*A. tetramera* excluded) as occurring naturally, and as being common where human disturbance has brought into contact different species; he reports that hybrid individuals appeared fertile. Zimmerman (1938, 1941) reports obtaining fertile hybrids of *A. triloba* (female) with *A. obovata*, *A. incana* and *A. longifolia* (syn, *A. angustifolia*). Swartz crossed *A. pygmaea* with *A. triloba* pollen, producing seed which failed to germinate (Peterson, 1986). In spring 1989, the author easily crossed *A. triloba* with pollen from *A. obovata*, *A. reticulata* and *A. parviflora*, and crossed *A. parviflora* with pollen from *A. triloba*; the success rate was about 50 percent, followed by normal fruit and seed development (germination has not been ascertained as of the time of this writing). Thus, all species of *Asimina* have been shown to cross easily with *A. triloba* except *A. tetramera* which has not been tested. The potential contributions of all 8 species to pawpaw improvement are summarized in Table 5.

Another possibility for improvement in pawpaw exists in wider crosses between *Asimina* and other genera in Annonaceae, notably *Annona*. A succinct and provocative discussion of the breeding possibilities in Annonaceae was published by Clift (1977), although others have also mentioned the possibility of using the *Annona* genus in the improvement of *A. triloba* (Amer. Genet. Assn., 1917; Zimmerman, 1940). The traits Clift identified within *Annona* as potentially valuable were fruit quality (especially flavor and aroma), adaptedness to dry soils, tolerance of saturated soils, bright skin colors, bright flesh colors, thick skin, compact growth habits, and hardiness. The degree of difficulty to be encountered in achieving *Asimina x Annona* crosses is unknown. Taxonomically, *Annona* belongs to the same tribe as *Asimina*, Unoneae, but to the other subtribe, Annonineae (Hutchinson, 1964). In addition to different climatic adaptations, the two genera differ most noticeably in the structure of their fruits: *Annona* fruits are compound, whereas *Asimina* fruits are simple. Both genera are very similar in pollination biology: flowers are strongly protogynous with

Table 5. Potential sources of germplasm for solving problems of genetic significance in *Asimina triloba.*

PROBLEM	*Asimina* species[1]							
Solution trait	TRI	PAR	RET	INC	PYG	TET	LON	OBO
DELAYED BEARING								
Precocity	X[2]	X	X	X	X		X	X
POOR YIELDS								
More floriferous	X	X	X	X	X	X	X	X[3]
Higher pollination rate	X	X			X			
Self-compatibility		X						
'Dwarf internode' trait					X			
Resists *T. plummeriana*								X[3]
HARVESTING COSTS								
Dwarf stature	no	X	X	X	X!	X	X	X
Better fruit visibility								
– horizontal leaves	X	X	X	X	X		X	X
– higher skin color	X							X
– late ripening fruit	X							X[3]
SEEDINESS OF FRUIT								
Fewer seeds per fruit	X	X	X	X	X		X	X
Smaller seeds	X	X	X	X	X		X	no
Lower seed: fruit ratio	X	no	no	no	no		no	no
FRUIT FRAGILITY								
Thicker, harder skin	X	X	X	X!	X		X!	X
Firmer flesh	X							
FRUIT PERISHABILITY								
Reduced metabolism	X							
Ability to be picked at earlier ripeness	X							

Table 5. Continued

PROBLEM Solution trait	TRI	PAR	RET	INC	PYG	TET	LON	OBO
	Asimina species[2]							
AESTHETIC								
Reduced skin bruising	X							
Higher skin coloration								
– whitish	X							X
– plum	X							X
– lavender								X
– yellow	X							
Showy, fragrant blossoms			X	X			X	X

[1] The species have been abbreviated to the first three letters of their epithet.
TRI = *A. triloba*, PAR = *A. parviflora*, RET = *A. reticulata*, INC = *A. incana*,
PYG = *A. pygmaea*, TET = *A. tetramera*, LON = *A. longifolia*, OBO = *A. obovata*.

[2] X = present, no = absent, (blank) = unknown.

[3] *A. obovata*'s terminal flowering habit may result in a lower blossom density. By blooming later in the season *A. obovata* may miss predation by *Talponia plummeriana* larvae, and its fruit may ripen relatively late.

similar pollen grains; the structure of the pistil is the same and presents no apparent barriers to the growth of the pollen tubes on route to the embryo sac (Lampton, 1952; Vasanthe Vithanage, 1982). Seed development and seed anatomy are very similar (Mohana Rao, 1982). A potential impediment to hybridization is a difference in chromosome number: for *Asimina* 2n = 18 whereas for *Annona* 2n = 14 (Darlington and Wylie, 1955). Zimmerman (1941) attempted, but failed, to hybridize *A. triloba* with *Annona squamosa* L. and *A. x atemoya.*

Potential benefits

The germplasm has been collected to allow the rapid development of high quality pawpaw cultivars. This, together with recent market developments, should support pawpaw cultivation. In 1989, a Michigan marketing cooperative sold wild-harvested pawpaws to a few select restaurants, and a major West Coast distributor of specialty produce received pawpaws for their evaluation. The Burpee Company now offers container-grown pawpaws, and is promoting them with attractive photos and accurate information. In the next 10 years, the general public will probably form their opinion of pawpaws. If they like what they see and taste, the pawpaw's market niche will be secure. If they are turned off by mediocre wild pawpaws of inferior flavor, seediness and looks, then pawpaw breeders will face an uphill battle to win the public confidence.

The opportunities for applied research related to the pawpaw will be many. Because of the pulp's unusual properties (highly viscous and hydrophilic, very potent in fruity volatiles, and free of browning reaction on exposure to air), food technologists may want to investigate its potential as a thickener, a flavoring agent, and a cosmetics base. Pharmacologists and chemists may seek to identify economical methods of extracting the pharmacological and insecticidal compounds in the seeds, and of detoxifying the otherwise highly nutritious seed meal. Botanists, entomologists, and plant physiologists may wish to describe the pollinators and the pollination biology of the flowers, and the postharvest physiology of the fruit. With proper plant breeding and scientific research, superior pawpaw cultivars will be developed, markets will be expanded, and pawpaws may become a popular new fruit that is cultivated in temperate regions around the globe.

Germplasm maintenance

At present, elite germplasm of *Asimina* is maintained by amateurs (in the Northern Nut Growers Association and the North American Fruit Explorers), by two institutions (the University of Maryland and the Blandy Experimental Farm of the University of Virginia), and by benign neglect. No formal program of pawpaw germplasm preservation exists. An extensive collection of germplasm is in the custody of the University of Maryland, consisting of over 1200 open-pollinated seedlings from the historic collections of Buckman, Zimmerman, Hershey, Allard, and the Blandy Experimental Farm, plus some miscellaneous sources. However, as this collection is intended as a plant breeder's working collection, it will not serve adequately the purposes of germplasm maintenance. The U.S.A. national clonal germplasm repositories are adequate to the task of maintenance, but at the present the pawpaw is too new, too minor, and too unproven to justify its inclusion in the system – particularly in light of the system's overstretched resources.

Fig. 1. Nature fruit on 1-year old *Asimina triloba* in the Wye collection, Maryland, U.S.A.

Summary and conclusions

The pawpaw has progressed from a condition 500 years ago of incidental and specialized domestication, to the point today where, if suitable markets and cultivars are developed, the interest in and use of the pawpaw may increase dramatically, and the pawpaw may become agriculturally domesticated. The systematic collection of superior pawpaw varieties began in 1916, initiated by a national contest. It has been built upon by a small group of horticulturalists who had sufficient vision and knowledge to exploit the raw material. During the same period scientific investigations were slowly accumulating information and knowledge about the pawpaw, primarily because of its singular status as the sole temperate genus of the Annonaceae. These converging developments and several cultural developments, such as the importance of fruit grown without pesticides, the vulnerability of genetic resources, the role of nutrition in human health, and the potential for new crops, has focussed greater attention on the pawpaw than at any previous time. As might be expected, a number of problems exist. However, their solution is feasible through conventional plant breeding and with the aid of mechanical and cultural methods. Fortunately, most of the genetic traits needed to improve the pawpaw are available in the collected germplasm. The prospect for rapid improvement is great.

It must be admitted, though, that the domestication of a new fruit crop adapted to the temperate zone cannot rank high in the list of total human needs in the late 20th century. Many needs are more pressing: the economic development of poor regions, the protection of the environment, the preservation of species and ecosystems, the development of human potential and human creativity. The addition of the pawpaw to the library of human agricultural domestics does little to further those aims. Although it is nutritious and high in calories, because it is a temperate climate species and perishable, it cannot improve the diets of the malnourished who reside mostly in the tropics. What the domestication of the pawpaw does, is remind us of the great possibilities that still remain for the agricultural domestication of new plant species.

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