

The Pawpaw, a Forgotten North American Fruit Tree

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The number of fruit trees native to North America is low compared to the many cultivated fruit species of Eurasian origin that currently form the basis for most fruit production in the New World. But there are a number of North American species with commercial possibilities, although many are neglected. Examples include a range of berries such as lowbush and highbush blueberries (*Vaccinium angustifolium* and *V. corymbosum*), cranberries (*V. macrocarpon*), huckleberries (*V. membranaceum*), American persimmon (*Diospyros virginiana*), American plum (*Prunus americana*), pawpaw (*Asimina triloba*), red mulberry (*Morus rubra*), and juneberries (*Amelanchier* spp.), most of them only available at a very small scale in some local markets. Among them, the pawpaw is probably one of the most interesting of the native North American fruit trees because of its exotic-tasting fruit and easy cultivation.

The History of Pawpaw

The earliest written report of pawpaw was made in 1541 by a Portuguese officer who was a member of Spaniard Hernando de Soto's expedition through the southeastern United States. He noted Native Americans growing and eating pawpaws in the Mississippi Valley region (Pickering 1879; Sargent 1890): "There is a fruit through all the country which groweth on a plant like Ligoacan [possibly a reference to *lignum vitae*, *Guaiaacum officinale*], which the Indians do plant. The fruit is like unto Peares Riall ["pears royal"]; it has a very good smell, and an excellent taste" (Hackluyt 1609). Apparently, the name pawpaw was given to the tree by the members of the de Soto expedition for the resemblance of the fruits to the tropical fruit papaya (*Carica papaya*) that they already knew (Sargent 1890), papaya being a Spanish word derived from the Taíno word *papaia*. In

some English speaking countries, such as Australia and New Zealand, the tropical papaya is also known as pawpaw, often resulting in confusion between the two species.

After this first report, pawpaw was described in records from additional explorations of the United States. One quote about the pawpaw in the northern United States is found in the so-called de Cannes memoir of 1690 (Pease and Werner 1934), probably written by Pierre Deliette, a French trader and colonial official who lived for several decades in Illinois: "There were other trees as thick as one's leg, which bend under a yellowish fruit of the shape and size of a medium-sized cucumber, which the



The name "pawpaw" was apparently derived from papaya (*Carica papaya*), seen here, a tropical fruit that has a slight resemblance to pawpaw fruit.



savages call *assemina*. The French have given it an impertinent name. There are people who would not like it, but I find it very good. They have five or six nuclei [seeds] inside which are as big as marsh beans, and of about the same shape. I ate, one day, sixty of them, big and little. This fruit does not ripen till October, like the medlars." In 1709, John Lawson, a British explorer, reported in his book *A New Voyage to Carolina*—probably the first report of pawpaw in English—that "The Papau is not a large tree. I think I never saw one a foot through; but has the broadest leaf of any tree in the Woods, and bears an apple about the bigness of a hen's egg, yellow, soft, and as sweet as anything can well be. They [the Indians] make rare puddings of this fruit" (Lawson 1709). English naturalist Mark Catesby described and illustrated the pawpaw in his classic 1754 edition of *The Natural History of Carolina, Florida, and the Bahama Islands*: "The trunks of these trees are seldom bigger than the small of a man's Leg, and are about ten or twelve feet high, having a smooth greenish brown Bark. In March when the leaves begin to sprout, its blossoms appear, consisting each of six greenish white petals, the fruit grows in clusters of three, and sometimes four together; they are at first green, and when ripe yellow, covered with a thin smooth skin, which contains a yellow pulp, of a sweet luscious taste; in the middle of which lye in two rows, twelve seeds divided by so many thin membranes. All parts of the tree have a rank, if not a foetid smell" (Catesby 1754). In 1749, the Jesuit priest Joseph de Bonnacamps described the pawpaw: "Now that I am on the subject of trees, I will tell you something of the assimine-tree, and of that which is called the lentil-tree. The 1st is a shrub, the fruit of which is oval in shape, and a little larger than a bustard's egg; its substance is white and spongy, and becomes yellow when the fruit is ripe. It contains two or three kernels, large and flat like the garden bean. They have each their special cell. The fruits grow ordinarily in pairs, and are suspended on the same stalk. The French have given it a name which is not very refined, *Testiculi asini*.

This is a delicate morsel for the savages and the Canadians; as for me, I have found it of an unendurable insipidity" (Thwaites 1899).

Besides these early reports, it is known that George Washington planted pawpaws at this home, Mount Vernon, in Virginia (Washington 1785). Pawpaws were also among the many plants that Thomas Jefferson cultivated at Monticello, his home in Virginia (Betts et al. 1986); during his time as Minister to France he had pawpaw seeds (Jefferson 1786) and plants (Jefferson 1787) shipped to his friends in Europe. In September 1806, the members of the Lewis and Clark expedition subsisted almost entirely on wild pawpaws for several days. William Clark wrote in his journal: "Our party entirely out of provisions. Subsisting on poppaws. We divide the buiskit which amount 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 the pap-paws" (Lewis and Clark 1806). Daniel Boone and Mark Twain were also reported to have been pawpaw fans (Pomper and Layne 2005), and early settlers also depended partially on pawpaw fruits to sustain them in times of crop failure (Peterson 1991). Pawpaws are well established in American folklore and history (the traditional American children's song, "Way down yonder in the pawpaw patch," is still popular) and several towns, creeks, and rivers have been named after this fruit tree.

Taxonomy, Origin, and Dissemination

The first fossils of *Asimina* have been dated to the Eocene (about 56 to 34 million years ago) and the first clearly resembling *A. triloba* to the Miocene (about 23 to 5.3 million years ago) (Berry 1916). Janzen and Martin (1982) hypothesized that large fruits produced by some Central American plant species were dispersed by large mammals that were extinct by the end of the Pleistocene; they extrapolated this observation to North American plants that produce large fruits, such as the pawpaw. With the extinction of the fruit-eating megafauna, the range

Naturalist Mark Catesby used flower and fruit specimens preserved in alcohol to create his illustration of pawpaw, which may explain the lack of maroon flower coloration in this depiction. Image courtesy Missouri Botanical Garden, www.botanicus.org



C.E. Faxon del.

Picart fr. sc.

ASIMINA TRILOBA, DUNAL.

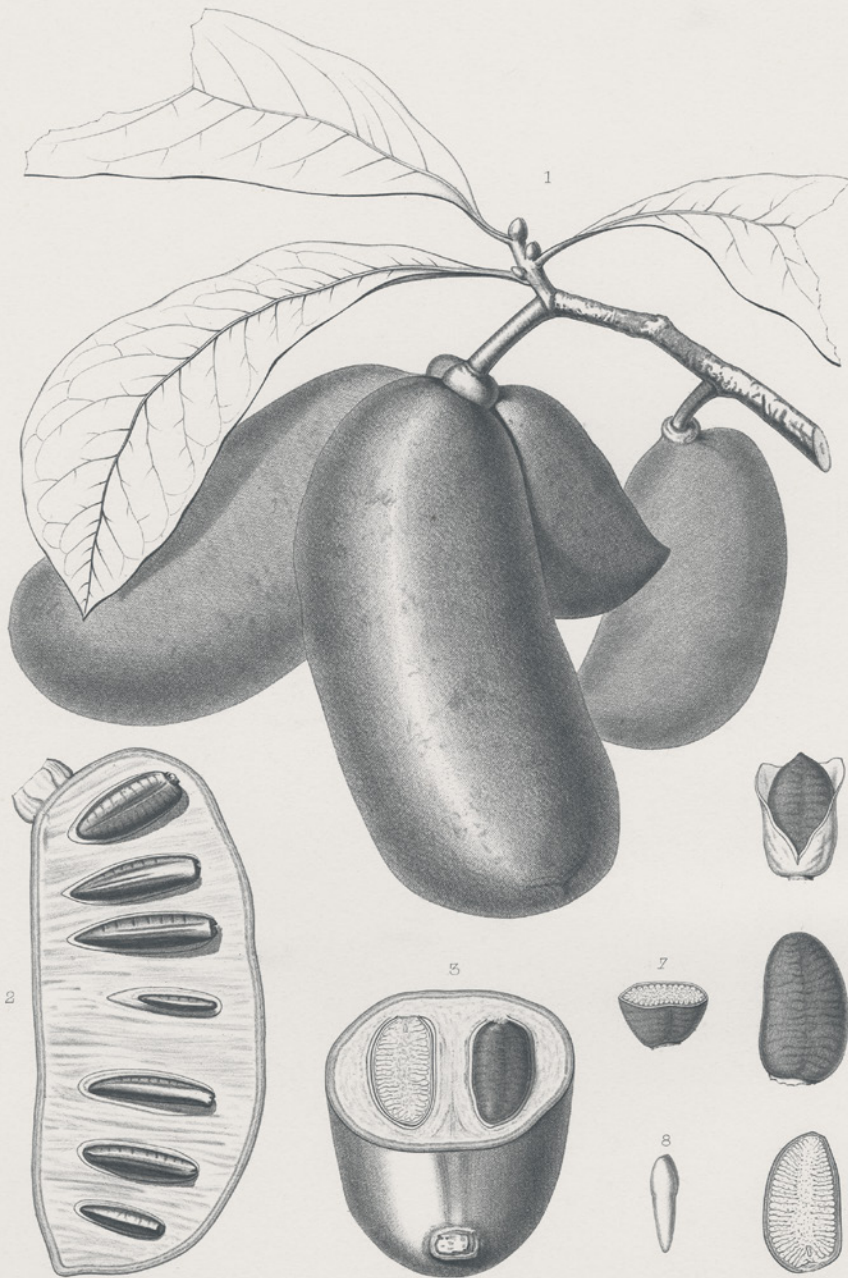
A. Riverous dixca!

Imp. R. Tancour, Paris.

Charles Edward Faxon's illustrations of *Asimina triloba* from Charles Sprague Sargent's *Silva of North America*, 1890.

Silva of North America.

Tab. XVI.



C.B.Faxon del

Picart fr. sc.

ASIMINA TRILOBA, Dunal

A. Fournier direx^t

Imp. R. Tonnau, Paris.

of the plant species dispersed by those animals started narrowing. Pawpaw probably survived thanks to its ability to easily reproduce vegetatively, producing numerous root suckers that form pawpaw patches in the wild (Barlow 2000, 2001). After the last ice age, humans could have become the new main vector dispersing pawpaw seeds and probably started the selection of plants with superior characteristics (Peterson 1991). Keener and Kuhns (1997) suggested that the northernmost distribution of the pawpaw into southern Ontario and western New York, Ohio, and Michigan was attributable to Iroquois population movements. Murphy (2001), however, argued against that hypothesis, suggesting instead that the spread of pawpaw could have been mainly by means of other mammals that seem to be able to eat pawpaw fruits, including raccoons, squirrels, opossums, foxes, bears, and white-tailed deer.

The North American pawpaw, *Asimina triloba* (L.) Dunal, is the northernmost representative of the mainly tropical and subtropical family Annonaceae, the largest living family within the order Magnoliales in the Eumagnoliid clade among the early-divergent angiosperms (Bremer et al. 2009). Annonaceae has more than 130 genera and 2,400 species (Couvreur et al., 2011), 900 of which are found in the Neotropics (Chatrou et al. 2004). Some of the tree species in the family such as cherimoya (*Annona cherimola*), sugar apple (*A. squamosa*), soursop (*A. muricata*), custard apple (*A. reticulata*), and atemoya (a hybrid between *A. cherimola* and *A. squamosa*) produce edible fruits, some of which were already used as a food source by pre-Columbian cultures in Central and South America (Popenoe 1989).

Pawpaw's scientific name has been changed repeatedly. Linnaeus first classified the pawpaw as *Annona triloba* in 1753. In 1763, Michel Adanson, a French naturalist, named the genus *Asimina* in his book *Familles naturelles des plantes*. The name *Asimina* is adapted from the native Algonquian word *assimin/rassimin/racemin*, via Cajun French *assiminier* (Chamberlain 1902; Gray 1886; Sargent 1890). Another North American native fruit, the American persimmon, also has the same root in its name, "min", the Algonquian word for fruit. However,



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The fruit of cherimoya (*Annona cherimola*).

in 1803 Michaux reclassified the pawpaw as *Orchidocarpum arietinum* and in 1807 Persoon reclassified it as *Porcelia triloba*. In 1817 Dunal renamed the species *Asimina triloba*. Torrey and Gray later moved the species to the genus *Uvaria*, but it was finally returned to *Asimina* by Gray in 1886 (Kral 1960). The current accepted nomenclature for the pawpaw is *Asimina triloba* (L.) Dunal.

The *Asimina* genus includes eight species native to North America (Kral 1960; Callaway 1990; Brett and Callaway 1992), four of which (*A. obovata* [Willd.] Nash, *A. pygmaea* [W. Bartram] Dunal, *A. reticulata* Shuttlw. ex Chapman, and *A. tetramera* Small) are found only in Florida, two (*A. incana* [W. Bartram] Exell and *A. longifolia* Kral) in Florida and southern Georgia, while *A. parviflora* (Michx.) Dunal reaches farther north, ranging from western Texas to North Carolina (Kral 1997). *Asimina triloba* is the most widespread of the eight species, indigenous to 26 states in the eastern United States,

ranging from New York, and southern Michigan on the north, south to northern Florida, and west to eastern Texas, Nebraska, and Kansas (Callaway 1990). It is also present in Ontario, Canada (Fox 2012).

A Description of Pawpaw

The pawpaw is the only species in the *Asimina* genus that produces fruits of significant interest as a food source. It is, in fact, the largest edible fruit native to North America. It grows wild as a deciduous understory tree in hardwood forests with moist but well-drained and fertile soils in the eastern United States, often in large patches of the same genotype due to extensive root suckering (Kral 1960; Pomper and Layne 2005), although sometimes different genotypes can be found in the same patch (Pomper et al. 2009).

Pawpaw trees can reach up to 10 meters (32.8 feet) tall and typically have a pyramidal habit in sunny locations. Pawpaw can be grown successfully in USDA plant hardiness zones 5 through 8 (average annual minimum temperatures -20 to 20°F [-28.8 to -6.7°C]) (Kral 1960). Pawpaw flower buds are dark brown, pubescent, and occur singly on the previous year's growth (Kral 1960). The flowers are light green upon emergence, but gradually turn maroon, with a slightly fetid aroma. The mature flowers are

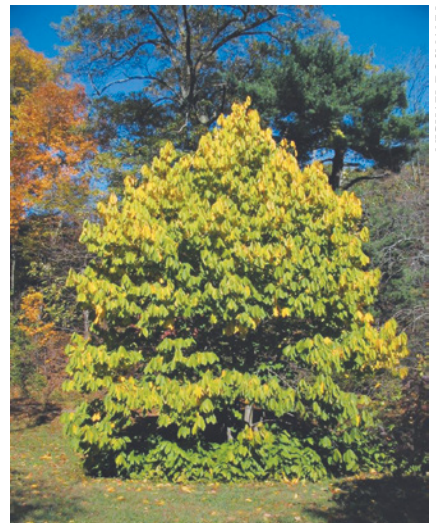


NANCY ROSE

A multitude of root suckers rise around the base of a pawpaw tree.

IN THE ARNOLD ARBORETUM there are currently four *Asimina triloba* specimens obtained from different sources:

- The oldest accession is 12708-A, grown from seeds sent by E. J. Cole of Grand Rapids, Michigan, in February 1903; records show that it was growing in its current location in 1926.
- 1222-79-A was collected from the wild as a plant by Arboretum staff members Jack Alexander and Gary Koller in Missouri in December 1979. It grew in the nursery for a few years and then was planted in the collection in 1986.
- 143-94-B was collected as seed in Michigan in October 1993 by Tim Boland (current director of the Polly Hill Arboretum in Martha's Vineyard). The seeds were received in early 1994 and one of the seedlings was planted in its current location in 2003.
- 205-91-A was collected as seed by staff members of the University of Guelph Arboretum (Ontario, Canada) in the floodplain of the Thames River in Middlesex County, Ontario. It was planted in the collection in 2003.



MICHAEL DOSMANN

Asimina triloba accession 1922-79-A in autumn.

2 to 5 centimeters (0.8 to 2 inches) in diameter, with 3 outer petals, 3 smaller inner petals, and 3 sepals. Flowers emerge before the leaves have emerged and expanded.

The flowers have a globular androecium and a gynoecium with 7 to 10 simple, uniloculate carpels (Lampton 1957). As with other species in the Annonaceae, pawpaw flowers show protogynous dichogamy, that is, the stigmas are receptive before pollen is released from the anthers, which often prevents self pollination. Most pawpaw cultivars are believed to be self-incompatible (Pomper and Layne 2008).

The pawpaw fruits are botanically berries (Dirr 1990). The fruits are sweet, highly nutritious, have a pleasant but strong aroma, and have a unique exotic taste that resembles a combination of banana, mango, and pineapple (Pomper and Layne 2005). The pulp can be

consumed both fresh and processed in different ways (ice cream, compotes, jam, pies, custards). The fruit can weigh up to 500 grams (17.6 ounces), with the average fruit weighing around 150 to 200 grams (5.3 to 7.1 ounces); there can be significant fruit weight differences depending on the genotype (Pomper and Layne 2005). The fruits have two rows of seeds with a total of 12 to 20 seeds that can be up to 3 centimeters (1.2 inches) long (Pomper and Layne 2008).

As with other Annonaceae species and other early-derived angiosperm families, pawpaws are primarily pollinated by flies and beetles that are attracted to the decaying smell and dark red color of the pawpaw flower; however, these pollinators are unreliable (Faegri and van der Pijl 1971) and often of limited availability resulting in low fruit yields both in wild stands and in cultivation (Pomper and Layne 2008).

NANCY ROSE



Flowers, foliage, and fruit of pawpaw.



A female zebra swallowtail oviposits on an emerging pawpaw leaf.

Butterflies, Pawpaw, and Coevolution

The zebra swallowtail (*Protographium marcellus*, formerly *Eurytides marcellus*) is a beautiful black and white striped butterfly whose caterpillars feed exclusively on *Asimina* leaves. (The damage made to the leaves is reported to be negligible in pawpaw orchards [Pomper and Layne 2008]). Some compounds present in the pawpaw leaves (acetogenins, specific substances only found in species of the Annonaceae) are repellent to most insects and birds so the caterpillar accumulates them to avoid predation. These natural bioactive compounds present in the leaves, bark, and twigs of pawpaw and other species of the Annonaceae have shown some insecticidal and anti-tumoral properties (McLaughlin 2008). Of the seven swallowtail tribes, the Graphini (to which the zebra swallowtail belongs) is one of the largest with about 150 species restricted to the tropics and subtropics except for two, *Iphiclides podalirius* and *Protographium marcellus* (the zebra swallowtail), that live in Palearctic and Nearctic regions, respectively (Haribal and Feeny 1998). The fact that both the zebra swallowtail and the pawpaw are the only members of their respective groups to live in temperate North America indicates that both species have coevolved and provides a neat system to study coevolution and adaptation to cooler climates.

The Current State of the Pawpaw

There was an increased interest in growing pawpaw as a crop at the beginning of the twentieth century; for example, in 1916 the American Genetic Association offered a \$100 prize—\$50 for the largest individual pawpaw tree and \$50 for the tree—regardless of size—with the best fruit (American Genetic Association 1916). Yet in spite of its high potential through the years as a new high-value niche fruit crop, pawpaw is still only in the early stages of commercial production. The greatest current market potential for pawpaw is probably in local markets and direct sales to restaurants and other gourmet niche customers. Most pawpaw fruits are



Illustration of the exterior and interior of a pawpaw fruit painted by Royal Charles Steadman in 1924. From the USDA Pomological Watercolor Collection in the Rare and Special Collections of the National Agricultural Library in Beltsville, Maryland.

still collected from wild stands or produced in small family orchards. Current pawpaw production challenges have been reviewed by Pomper and Layne (2005) and include the need for new high-quality cultivars, pollination improvement, and postharvest issues; the shelf life of a tree-ripened fruit stored at room temperature is just 2 to 3 days, although under appropriate refrigeration conditions fruits harvested before fully ripening can be held up to 3 weeks while maintaining good eating quality. A number of high-quality pawpaw cultivars with large fruit (over 5 ounces) and heavy production have been selected since 1950 at Kentucky State University, which serves as a USDA National Clonal Germplasm Repository for *Asimina* species (Willson and Schmeske 1980; Pomper and Layne 2005).

Though pawpaws may never be as popular as apples or oranges, perhaps one day they'll at least make it out of the pawpaw patch and into the local grocery store. If you don't want to wait for that to occur, consider planting some pawpaw trees in your own backyard. This will give you the opportunity to taste an exotic fruit native to North America and, at the same time, perhaps enjoy the visit of zebra swallowtails.

References

- American Genetic Association. 1916. Where are the best pawpaws? *Journal of Heredity* 7: 291–296.
- Barlow, C. 2000. *The Ghosts Of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms*. New York: Basic Books.
- Barlow, C. 2001. Anachronistic fruits and the ghosts who haunt them. *Arnoldia* 61: 14–21.
- Berry, E. W. 1916. *The lower eocene floras of southeastern North America*. United States Geological Survey, Professional Paper 91, p. 90.
- Betts, E. M., H. B. Perkins, and P. J. Hatch. 1986. *Thomas Jefferson's Flower Garden at Monticello*, 3rd edition. Charlottesville: University Press of Virginia.
- Bremer, B., K. Bremer, M. W. Chase, M. F. Fay, J. L. Reveal, D. E. Soltis, P. S. Soltis, and P. F. Stevens. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnaean Society* 161: 105–121.
- Brett, M. and D. J. Callaway. 1992. Our native pawpaw: the next new commercial fruit? *Arnoldia* 52(3): 21–29.
- Callaway, M. B. 1990. *The pawpaw (Asimina triloba)*. Kentucky State University Publications CRS-HORT1-901T.
- Catesby, M. 1754. *The Natural History of Carolina, Florida and the Bahama Islands*. London.
- Chamberlain, A. F. 1902. Algonquian words in American English. *Journal of American Folklore* 15: 240–267.
- Chatrou, L. W., H. Rainer, and P. J. M. Mass. 2004. Annonaceae. In: D. W. Stevenson, S. V. Heald, N. Smith, S. A. Mori, A. Henderson (eds.). *Flowering Plants of the Neotropics*. Princeton, New Jersey: Princeton University Press. pp. 18–20
- Couvreur, T. L. P., M. D. Pirie, L. W. Chatrou, R. M. K. Saunders, Y. C. F. Su, J. E. Richardson, and R. H. J. Erkens. 2011. Early evolutionary history of the flowering plant family Annonaceae: steady diversification and boreotropical geodispersal. *Journal of Biogeography* 38: 664–680.
- Dirr, M. A. 1990. *Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Culture, Propagation, and Uses*. 4th ed. Champaign, Illinois: Stipes Publishing.
- Faegri, K. and L. van der Pijl. 1971. *The Principles of Pollination Ecology*. New York: Pergamon Press.
- Fox, S. 2012. Picking up the pawpaws: the rare woody plants of Ontario program at the University of Guelph Arboretum. *Arnoldia* 69(3): 2–13.
- Gray, A. 1886. The genus *Asimina*. *Botanical Gazette* 11: 161–164
- Hackluyt, R. 1609. *A narrative of the expedition of Hernando de Soto into Florida. By a Gentleman of Elvas*. Published at Evora 1557. Translated from the Portuguese by Richard Hackluyt. London. <http://archive.org/details/anarrativeofthee34997gut> (accessed January 9th 2014).
- Haribal, M. and P. Feeny. 1998. Oviposition stimulant for the zebra swallowtail butterfly, *Eurytides marcellus*, from the foliage of pawpaw, *Asimina triloba*. *Chemoecology* 8: 99–110.
- Janzen, D. H. and P. S. Martin. 1982. Neotropical anachronisms: The fruits the gomphotheres ate. *Science* 215: 19–27.

- Jefferson, T. 1786. From Thomas Jefferson to John Bartram, with Enclosure, 27 January 1786, Founders Online, National Archives (<http://founders.archives.gov/documents/Jefferson/01-09-02-0201>, ver. 2013-08-02). Source: *The Papers of Thomas Jefferson*, vol. 9, 1 November 1785–22 June 1786, ed. Julian P. Boyd. Princeton: Princeton University Press, 1954, pp. 228–230.
- Jefferson, T. 1787. From Thomas Jefferson to John Banister, Jr., with enclosure, 7 February 1787," Founders Online, National Archives (<http://founders.archives.gov/documents/Jefferson/01-11-02-0122>, ver. 2013-08-02). Source: *The Papers of Thomas Jefferson*, vol. 11, 1 January–6 August 1787, ed. Julian P. Boyd. Princeton: Princeton University Press, 1955, pp. 121–122.
- Keener, C. and E. Kuhns. 1997. The impact of Iroquoian populations on the northern distribution of pawpaws in the Northeast. *North American Archaeologist* 18: 327–342.
- Kral, R. 1960. A revision of *Asimina* and *Deeringothamnus* (Annonaceae). *Brittonia* 12: 233–278.
- Kral, R. 1997. Annonaceae. In: *Flora of North America*. Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 16+ vols. New York and Oxford. Vol. 3, pp. 11–20.
- Lampton, R. K. 1957. Floral morphology in *Asimina triloba* Dunal, development of ovule and embryo sac. *Bulletin of the Torrey Botanical Club* 84: 151–156.
- Lawson, J. 1709. *A New Voyage to Carolina*. London. <http://docsouth.unc.edu/nc/lawson/lawson.html> (accessed January 9th 2014).
- Lewis, M. and W. Clark. 1806. September 18, 1806, entry in *The Journals of the Lewis and Clark Expedition*, ed. Gary Moulton. University of Nebraska Press. 2005. http://lewisandclarkjournals.unl.edu/read/?_xmlsrc=1806-09-18&_xslsrc=LCstyles.xsl (accessed January 9th 2014).
- McLaughlin, J. L. 2008. Paw Paw and cancer: annonaceous acetogenins from discovery to commercial products. *Journal of Natural Products* 71: 1311–1321.
- Murphy, J. L. 2001. Pawpaws, persimmons, and 'possums: on the natural distribution of pawpaws in the northeast. *North American Archaeologist* 22: 93–115.
- Pease, T. C. and R. C. Werner. 1934. *The French Foundations, 1680–1693*. Illinois Historical Collections, XXIII. Springfield: Trustees of the Illinois State Historical Library.
- <https://archive.org/details/frenchfoundation23peas> (accessed January 9th 2014).
- Peterson, R. N. 1991. Pawpaw (*Asimina*). *Acta Horticulturae* 290: 569–602.
- Pickering, C. 1879. *Chronological History of Plants*. Vol. 1. Boston: Little, Brown and Company.
- Pomper, K. W. and D. R. Layne. 2005. The North American pawpaw: botany and horticulture. *Horticultural Reviews* 31: 351–384.
- Pomper, K. W. and D. R. Layne. 2008. *Asimina triloba*, pawpaw. In: J. Janick and R. E. Paull (eds.). *The Encyclopedia of Fruits and Nuts*. CAB International, pp. 62–68.
- Pomper, K. W., J. D. Lowe, L. Lu, S. B. Crabtree, and L. A. Collins. 2009. Clonality of pawpaw (*Asimina triloba*) patches in Kentucky. *Journal of the Kentucky Academy of Sciences* 70: 3–11.
- Popenoe, H. 1989. *Lost Crops of the Incas: Little Known Plants of the Andes with Promise of Worldwide Cultivation*. Washington, D.C.: National Academy Press.
- Sargent, C. S. 1890. *Silva of North America*. New York: Houghton Mifflin.
- Thwaites, R. G. 1899. *The Jesuit Relations and Allied Documents*. Travels and explorations of the Jesuit missionaries in New France 1610–1791. Vol. LIX. Cleveland: The Burrows Brothers Publishers.
- Washington, G. 1785. Founders Online, National Archives (<http://founders.archives.gov/documents/Washington/01-04-02-0002-0003>, ver. 2013-08-02). Source: *The Diaries of George Washington*, vol. 4, 1 September 1784–30 June 1786, ed. Donald Jackson and Dorothy Twohig. Charlottesville: University Press of Virginia. 1978. pp. 96–111.
- Willson, M. F. and D. W. Schmeske. 1980. Pollinator limitation, fruit production, and floral display in Pawpaw (*Asimina triloba*). *Bulletin of the Torrey Botanical Club* 107: 401–408.

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