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Diversity of Pawpaw *(Asimina triloba)* Cultivars in USDA Repositories and Selected Retail Nurseries c. 2022

Richard B. Frost

Additional index words: ancestry, fruit weight, genomic-morphologic associations

Abstract

This study reviewed available data for Pawpaw (*Asimina triloba*) cultivars in the U.S. with the goal of determining genetic diversity and genomic-morphologic relationships. Ninety cultivars available at U.S. retail sites and 20 cultivars at USDA sites (6 unique from retail) in 2022 are listed. Nine genetic studies of pawpaw are then reviewed, finding 17 genetic associations among the retail cultivars. Recent agricultural, chemical, tensile, and spectrometric morphology data are also reviewed. An association with larger fruit weight and cultivars derived from 'Middletown' was found, but the remaining forms of morphology data were either uncorrelated with genomic data or otherwise unsuitable to determine genomic associations. A discussion of criteria for future genomic-morphologic studies of *Asimina triloba* is also included.

Over the last 140 years the development and preservation of U.S. Pawpaw (*Asimina triloba*) selections has passed through many hands, including J.A. Little, E.J. Downing, G..A. Zimmerman, O.E. White, G.L. Slate, C. Davis, J. Gordon, P. Thomson, R.N. Peterson, J. Lehman, and C. England (Davis, 1982; England, 2022; Little, 1905; Peterson, 1991; Peterson, 2003; Pomper et al., 2009; Thomson, 1974; Zimmerman, 1941). A few unusual cultivars are now appearing in the retail trade, including variegated 'Spilt Milk' plus three freestone cultivars 'Cantaloupe', 'Honey Dew', and 'Marshmallow'. Much has been written about the fruit in the last few decades, including food chemistry (Brannan et al., 2015; Grygorieva et al., 2021), propagation and planting guides (Cothron, 2021; Hummer, 2020; Tabacu et al., 2020), and ecotours (Moore, 2015). Interest in Pawpaw cultivation has also spread overseas (Brannan and Coyle, 2021). A list of cultivars currently held at USDA repositories is given in Table 1 and those presently available from U.S. retail nurseries in Table 2.

This report is part of a series involving genetic ID and genetic clades within lesser studied fruits. In tandem it has been discovered that unsound mathematical practices have found their way into mainstream bioinformatics and are currently considered valid by investigators and reviewers alike (Frost, 2022b). Several of the articles reviewed here are no exception. The primary issues encountered here are use of non-metric dissimilarities, pair-grouping, and use of data with missing values for distance. Note that "metric" here refers to the mathematical definition of distance – not units of measure. All three of these practices appear in biology curricula and consequently the authors cited here have used them unwittingly.

Materials and Methods

Genomic studies. Nine genomics studies of U.S. Pawpaw cultivar diversity have been conducted since 1990. Three were authored by H. Huang et al: the first primarily to determine an advanced set of RAPD markers (Huang et al., 2000), the second utilizing 71 RAPD markers on 37 cultivars (Huang et al., 2003), and the third using ALFP markers

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Table 1. List of cultivars currently held at USDA repositories (USDA, 2022).

Cultivar	Year introduced	USDA Repository Administration
Allegheny	2007	NCGR Corvallis
Ames 3129	1984	National Arboretum
Ames 32220	2014	North Central Regional PI Station
Ames 7465	1986	North Central Regional PI Station
Anniston	?	NCGR Corvallis
KSU Atwood	1990	NCGR Corvallis
KSU Benson	1990	NCGR Corvallis
Mango	1970	NCGR Corvallis
NA 82138	2014	National Arboretum
NA 83885	?	National Arboretum
NC-1	1976	NCGR Corvallis
Overleese	1950	NCGR Corvallis
PA Golden No. ?	1986	NCGR Corvallis
Potomac	1994	NCGR Corvallis
Prolific	1985	NCGR Corvallis
Shenandoah	1990	NCGR Corvallis
Susquehanna	1990	NCGR Corvallis
Taytwo	1968	NCGR Corvallis
Wabash	1994	NCGR Corvallis

(Wang et al., 2005). Unfortunately, all three applied a non-metric measure to determine dissimilarities. Of these the second publication contains all marker data but also suffered from missing marker values. A recent mathematics study has salvaged 45 from the set (Table 3), providing a coarse measure of genomic dissimilarity among the specimens (Frost, 2022a).

A second set of published studies are affiliated with Kentucky State University. The first study (Pomper et al., 2003) used questionable marker loci which under Jaccard's metric produces 4 sets of zero distances between cultivars known to have different parentage. The second (Pomper et al., 2010) is plagued by poor data quality and use of a non-metric dissimilarity measure. A comparison of genetic associations and clades found by Frost (2022a) and the second KSU study is shown in Table 4. The third study (Lu et al., 2011) used 20 SSR primer pairs but unfortunately did not publish their marker data. A fourth study (Botkins et al., 2012) used 6 standard SSR loci to estimate clonal variation in 7 localized wild or feral pawpaw patches but also did not publish the marker data.

An interesting undergraduate study from West Virginia University analyzed 19 unnamed specimens from 3 campus pawpaw patches for clonal variation using 12 ISSR microsatellite markers (Fontana, 2019). A heat map was used to visualize the inter-patch diversity, shown here in a topological graph (Figure 1). In 2021 a trio from the University of Georgia published a study of morphologic and microsatellite data from 20 U.S. sites associated with pre-Columbian settlements and 62 possibly wild specimen sites in the eastern U.S. (Wyatt et al., 2021). Unfortunately the investigators chose non-metric dissimilarity measures to analyze their data and the marker values contain numerous missing values (Table 5) making them unsuitable for any analysis (Schlueter and Harris, 2006).

Morphology studies. Several studies of pawpaw cultivar morphology data have been published in the past 20 years. Survival rates

Table 2. Cultivars available at some point in 2022 from one or more of the following U.S. retail sites: Cricket Hill Garden, Elmore Roots Nursery, England's Orchard, Hidden Springs Nursery, Just Fruits and Exotics, Kiefer Nursery NC, Nash Nurseries, One Green World, Peaceful Heritage Nursery, Perfect Circle Farm, Raintree Nursery, Red Fern Farm, Restoring Eden, Tollgate Gardens.

8-20	9-58-?	Al Horn White Flesh	Allegheny	Asterion	Atria
Avatar	Belle	Benny's Favorite	Betria	Canopus	Cantaloupe
Carmelo	Caspian	Cluster	Collins	Convis	Davis
Dr. Chill	Ford Amend	Free Byrd	Fulbright's Delight	Gainsville #1	Gainsville #2
Gatria	Golden Moon	Greenriver Belle	Halvin	Honey Dew	IXL
Jerry's Big Girl	Jerry's Delight	Kentucky Champion	KSU Atwood	KSU Benson	KSU Chappell
LA Native	Lady D	Lehman's Chiffon	Lehman's Delight	Lynn's Favorite	Mango
Maria's Joy	Marshmallow	Mitchell	MSU Golden	NC-1	Nyomi's Delicious
October Moon	Overleese	PA Golden No. ?	PA Golden No. 1	PA Golden No. 2	PA Golden No. 3
Potomac	Prima 1216	Prolific	Quaker Delight	Rappahannock	Rebecca's Gold
Regulus	Rigel	SAA-Overleese	SAA-Zimmerman-#?	Shenandoah	Sibley
Sidewinder	Spilt Milk Variegated	Sue	Summer Delight	Sunflower	Sunglo
Sunsprout	Susquehanna	Sweet	Sweet Alice	Sweet Potato	Sweet Virginia
Tallahatchie	Taylor	Taytwo	Tollgate	Tropical Treat	UVM #1
VE-21	Wabash	Walters	Wells	Windstar	Zimmerman

Table 3. Names of 45 RAPD marker primer sequences used in coupled analysis of pawpaw genetic markers and ancestry records (Frost, 2022a).

A07-1600	A07-0600	A11-0850	A11-0600	A11-0425	A12-0550	B07-1200	B07-0550	B08-0900
B09-0900	B10-1775	B10-1200	B10-0950	B10-0900	B11-0525	C02-0650	C04-1300	C04-1675
C04-1175	C08-0425	C11-1550	C13-1300	C15-1050	C15-0650	D05-1250	D05-0500	D05-0450
D05-0600	D05-0575	D15-0550	D15-0425	D16-1000	D16-0525	D16-0400	D16-0325	D20-0775
D20-1100	E01-0850	E01-0450	E11-1675	E14-0850	E15-0700	E16-0550	E16-1025	E17-0900

of specimens in irrigated and unirrigated orchards were recorded by investigators at Kentucky State University (Pomper et al., 2008). Of those in the irrigated plot for which there is also viable genomic data, only 'Overleese', 'Susquehanna', 'Taylor', and 'Wells' had survival rates in the range 75% to 88% and the remainder had no casualties. Average fruit weights at harvest were recorded by investigators at KSU, Ohio University, and North Carolina Cooperative Extension (Figure 2). The KSU investigators also contribut-

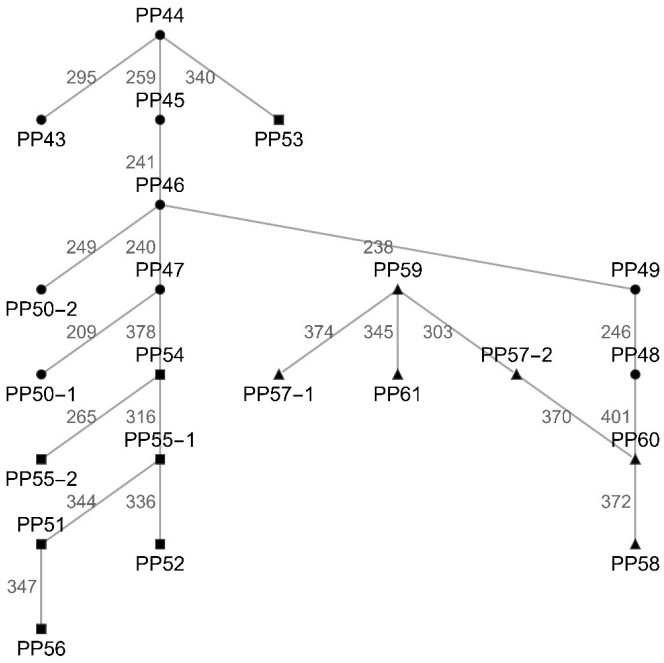

Figure 1. Genetic diversity among 19 numbered specimens from 3 separate pawpaw patches studied by K. Fontana (Fontana, 2019). Dissimilarity values computed by a metric in package GenAlEx (Peakall and Smouse, 2018) and plotted here in a least bridges graph (Frost, 2022b). Circle markers are from patch 1, squares are from patch 2, and triangles from patch 3. Spatial orientation and scale in the graph are arbitrary.

ed agriculturally important Growing Degree Days data (Pomper et al., 2008) (see Table 6). Measurements of interest in food science were taken in Ohio (Brannan et al., 2015) of 4 applicable cultivars (see Table 7).

Results

Genetic associations. Seventeen genetic associations determined from a reduced set of 49 RAPD markers (Frost, 2022a) are listed in column 3 of Table 4. However, the specimens in this study are a biased selection of *Asimina triloba* genomes and so the smallest association groups defined here should be taken with a grain of salt. More study is clearly needed to determine better methods of genetic discrimination among Pawpaw cultivars.

Genomic-morphologic connections. Possible connections between genomic and morphologic data were examined for this study. The small variances in survival rates were considered problematic for analysis. The phenolic and spectrometric data were also not analyzed due to caution in the study paper regarding different levels of ripeness among the specimens.

Hopes for finding a relationship between the Growing Degree Days (GDD) data and genomic groups were not met. Linear and multilinear models constructed from the KSU clades and genetic associations of this study returned correlation coefficients of -0.05, 0.09, and 0.098. The disparity between the marker groups and GDD data is illustrated in Figure 3.

Success occurred with comparisons of genomic data and vetted fruit weight data. The raw data originated in 4 separate studies as

Table 4. Comparison of genetic associations and clades determined by R. Frost[a] (Frost, 2022a) and investigators at KSU[b] (Pomper et al., 2010). The determination of genetic associations is illustrated in Figure 5. Pivots were selected for their independence and utility with other cultivars. Some of the groups are due to unique ancestors while others (e.g. 3-11) either share an unknown ancestor or a common set of chromosomal subsequences that have been reinforced by breeding programs.

Cultivar	Year introduced	In 2022 retail trade	Selected genomic pivots[a]	Genomic associations[a]	Primary association[a]	KSU clade[b]
Middletown	1915		X	A	A	IV
Prolific	1985	R		A	A	II
2-49	1990			A	A	untested
9-47	1990			A	A	III
Rappahannock	1990	R		A	A	III
Shenandoah	1990	R		A	A	V
Susquehanna	1990	R		A	A	II
5-5	1994			A	A	IV
7-90	1994			A	A	IV
Overleese	1950	R		ADF	A	V
Potomac	1994	R		ADF	A	III
3-21	1994			ADG	A	IV
2-54	1990			AEF	A	II
NC-1	1976	R		AF	A	V
2-10	1994			AG	A	II
Sweet Alice	1945	R	X	B	B	III
9-58-2	1994			B	B	untested
SAA-Zimmerman-1	1985			BA	B	untested
SAA-Zimmerman-2	1985			BDF	B	untested
Taylor	1968	R	X	C	C	I
Taytwo	1968	R		C	C	V
Wilson	1980s			C	C	I
Sunflower	1970	R	X	D	D	V
1-68	1994			D	D	V
Wabash	1994	R		D	D	III
8-20	1994	R		DB	D	II
Rebecca's Gold	1974	R	X	E	E	V
9-58-1	1990			E	E	untested
Wells-PPF	1990			E	E	untested
Mitchell	1979	R	X	F	F	V
PA-Golden	1986	R		F	F	untested
Wells	1990	R		F	F	IV
3-11	1994		X	G	G	II
11-13	1990			GA	G	II
10-35	1990			numerous	n/a	III
1-23	1990			numerous	n/a	V

Table 5. Percent missing values across sites, specimens, and markers in a population dispersal study at University of GA (Wyatt et al., 2021).

Site Population Types	Sites missing values	Specimens missing values	Marker alleles missing values
Anthropomorphic	70.0%	52.8%	61.1%
Wild	82.3%	70.1%	72.2%

Table 6. Measurements of GDD by KSU investigators (Pomper et al., 2008). Some of the estimated peak flowering weeks have been back-calculated from GDD and harvest week.

Cultivars in retail circulation	Estimated peak flowering week at KSU sites	GDD at KSU sites	Peak harvest week at KSU sites
PA-Golden	16	2499	36
Wabash	16	2572	36
Rappahannock	16	2586	36
NC-1	16	2620	37
Overleese	16	2637	37
Taytwo	16	2648	37
Taylor	16	2676	37
Shenandoah	16	2697	37
Susquehanna	16	2703	37
Potomac	16	2720	37
Mitchell	16	2736	37
Sunflower	16	2737	37
Wells	15	2751	37
8-20	15	2753	37

Table 7. Soluble solids concentrations, phenolic, tensile, and spectrometric measurements of pawpaw cultivars (Brannan et al., 2015) applicable to H. Huang's RAPD markers (Huang et al., 2003).

Cultivar	Soluble solids conc.	Phenolics (µmol/g)	pulp texture (kg)	skin CIE color (L*,a*,b*)	pulp CIE color (L*,a*,b*)
NC-1	25.7	5.68 ± 0.41	0.248	{62.9,-4.8,30.2}	{77.1,10.1,45.9}
Overleese	25.1	5.30 ± 0.17	0.198	{65.1,-8.8,33.0}	{79.3,2.1,34.6}
Rebecca's Gold	23.5	5.38 ± 0.67	0.415	{63.3,-7.8,35.2}	{75.1,6.7,42.0}
Taytwo	25.2	6.21 ± 0.20	0.363	{61.7,-6.0,29.6}	{71.2,12.2,53.2}

shown in Figure 2. The data were filtrated by making pairwise comparisons between the Greenawalt series and the others – under the assumption that fruit weights from different sites vary by linear proportion. For each pairwise comparison, a common ordinal specimen was selected, e.g. 'Overleese' compared to the Brannan and Greenawalt series. The percentage of weight change of each specimen from the ordinal was then calculated for

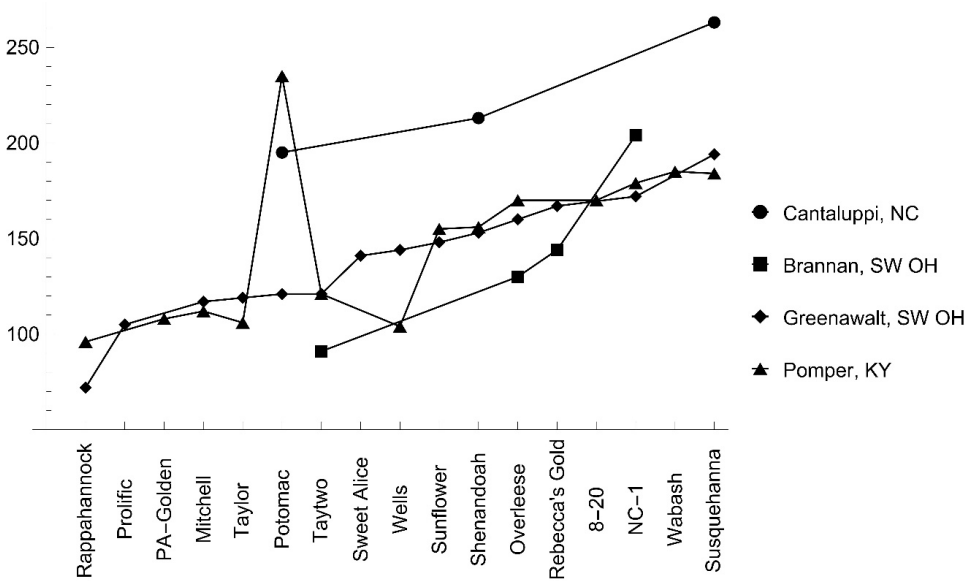

Figure 2. Fruit production data in average grams per fruit from Oxford NC, SW OH, and KSU sites in KY sorted by L. Greenawalt's SW OH data (Brannan et al., 2015; Cantaluppi and Coley, 2020; Greenawalt et al., 2019; Pomper et al., 2008).

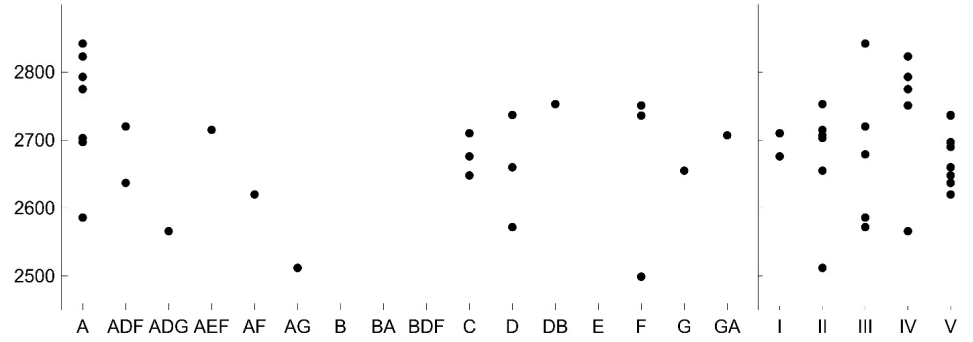

Figure 3. Disparity between GDD data and genetic marker groups.

each of the two series, e.g. the % gains for the Brannan series using 'Overleese' as ordinal are {-30%,0%,~10.8%,~56.9%}. The differences of percentage gain series were examined and any specimen pair with more than ±10% difference was rejected. For example, the series differences between Brannan and Greenawalt were approximately {-5.6%,0.%,6.4%,49.4%} and thus specimen 'NC-1' was eliminated from that pair of series. Any specimens for which there was no comparative value was also eliminated. Figure 4 illustrates the vetted results from all 4 studies. The vetted data was used to construct the genomic-morphologic comparison of Table 8. The influence of cultivar 'Middletown'

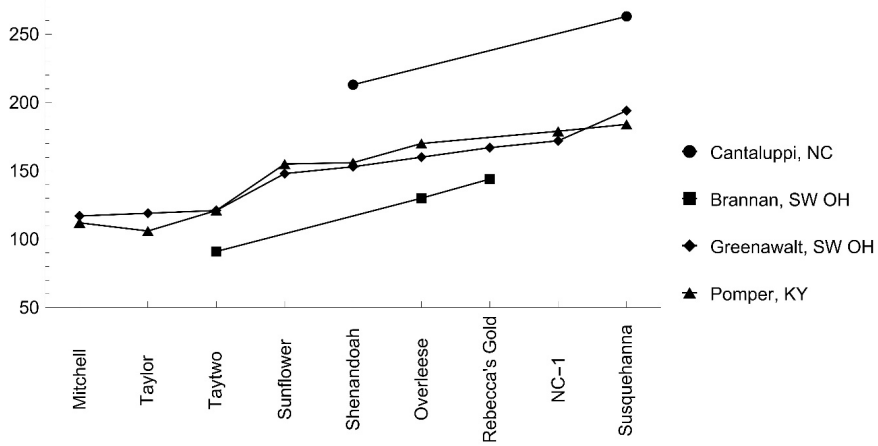

Figure 4. Vetted fruit weight (g) data extracted from Figure 2.

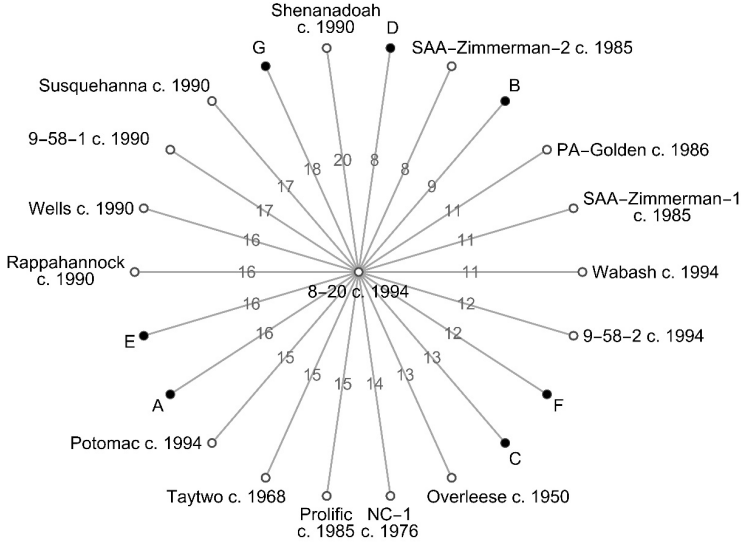

Figure 5. Illustration of genetic association selection for cultivar 8-20. Only genetic distances less than the sub-average distance of 12 mismatches were considered (see Figure 6). Spatial orientation and line segment lengths likely have no correlation to actual 45-dimensional space.

on higher fruit weights is apparent. The cultivar 'Taylor' and its possible sibling 'Taytwo' both appear in section of lower weights, as do 'Sunflower' and 'Mitchell'. These latter two are also present as minor components in the higher fruit weight specimens. One can speculate here that the influence of 'Middletown' is too dominant for them but a future study with more refined data is probably warranted.

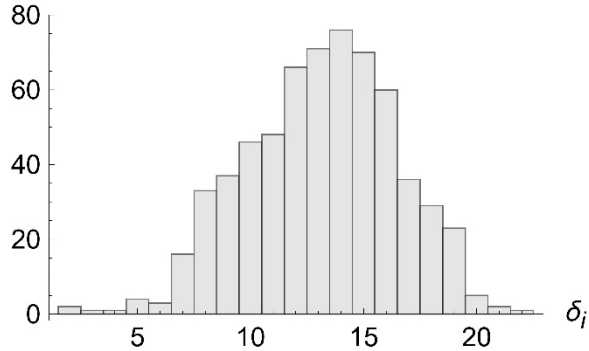

Figure 6. Sample distribution of marker mismatches in 36 unique specimens measured with 45 error-free RAPD markers of H. Huang (Frost, 2022a).

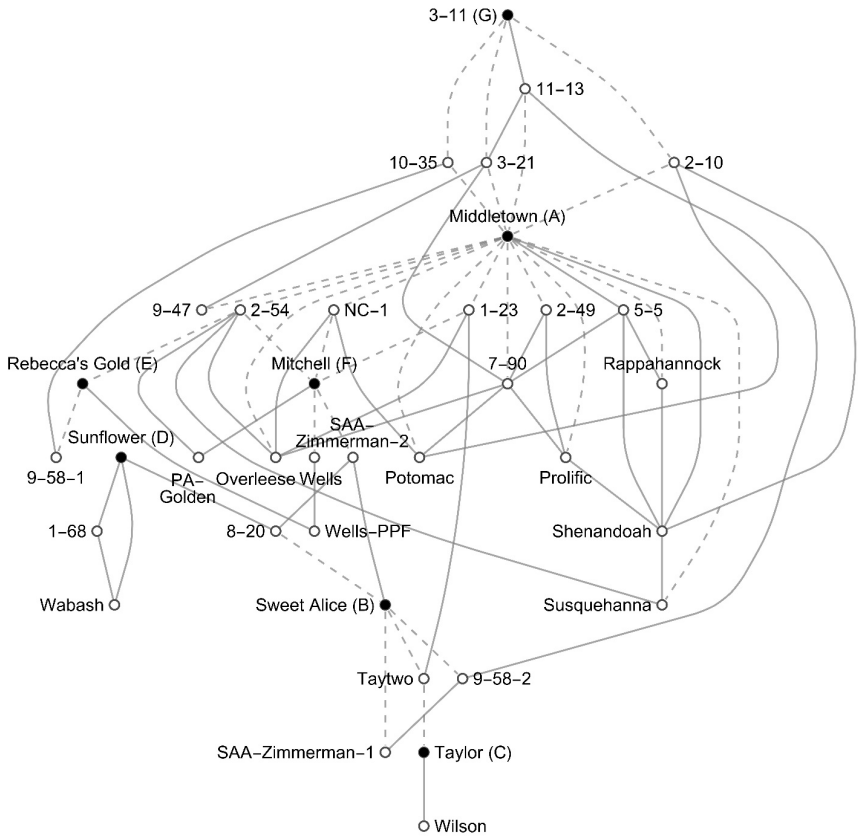

Figure 7. Topological graph of genomic associations among 36 Pawpaw cultivars of this study. Solid lines are nearest neighbor connections. Dashed lines are cultivar associations of genomic pivots determined by least bridges graph (Frost, 2022b). Line lengths and spatial orientation are arbitrary.

Table 8. Comparison of vetted average fruit weights with genomic groupings by R. Frost[a] (above) and KSU[b] (Pomper et al., 2008)

Fruit weights in SW Ohio (g)	Cultivar	Year introduced	Genomic associations[a]	KSU clade[b]
117	Mitchell	1979	F	V
119	Taylor	1968	C	I
121	Taytwo	1968	C	V
148	Sunflower	1970	D	V
153	Shenandoah	1990	A	V
160	Overleese	1950	ADF	V
167	Rebecca's Gold	1974	E	V
172	NC-1	1976	AF	V
194	Susquehanna	1990	A	II

Discussion

The specimens in the genomic studies of H. Huang (Huang et al., 2000; Huang et al., 2003) are for the most part closely related due to a century of breeding programs. This situation produces a condition of "too much cohesion" in topological graphs using metric distances (Frost, 2022b). As such, these graphs are difficult if not impossible to partition with standard graph theory methods. The approach taken here of genomic pivots (pseudo basis points) is one alternative (see Table 4 and Figure 5). However, the associations alone do not provide an adequate "map" of specimen relations. Figure 7 shows an attempt to resolve the issue with a hybrid graph, incorporating associations with nearest neighbor relations.

If the USDA online records are correct then the USDA germplasm repositories for *Asimina triloba* poorly represent genomic diversity in the species. One would expect specimens representing each of the genomic pivots identified above plus others selected for traits of agricultural interest. Viable genetic fingerprinting of the USDA collection would be beneficial.

The application of 45 markers from H. Huang's original set (Huang et al., 2003) to fruit weights show that they have merit beyond ancestral relations. Using the entire set of 71 on all cultivars in retail circulation could provide a more exacting view of diversity within the selections and guidance for future breeding. If the fingerprinting is to be effective, the RAPD data for each specimen needs to be composed of one error-free set or 5-8 sets with 10% or less missing values and enough overlap to produce a high-confidence correlated error-free set (Frost, 2022b).

If an investment is made in taking new genomic measurements, it would be highly beneficial to collect an array of morphologic data in-situ. Ripe fruit for laboratory assay should be obtained from each of the leaf specimen trees and some quantitative measure of "ripeness" should be made for registration of compound concentrations in the fruit samples (Brannan et al., 2015). Compounds of interest in the fruit include annonacins, carbohydrates, fruit sugars, flavonoids, glutamates, phenols, and proteins. Tensile tests should include skin shear strength and bulk texture. Average seed counts and percent by volume are desirable for selective breeding. Collection of harvest degree-days information (fruit set date, harvest date, tree location) and cultivar vigor would be a bonus. The testing of annonacin concentrations is important for understanding possible health risks of the fruit. A determination can be made by comparing annonacin concentrations to lifetime dosage limits for injectable annonacin used in contact treatment of can-

cer cells times the expected percent of drug escape into the patient blood stream.

Conclusions

Categorizing cultivar traits with genomic groupings in Pawpaw is difficult with currently available information. It has been demonstrated here that prior studies using RAPD analysis can only provide coarse group distinctions and that nearly all prior genomic studies are based on invalid mathematical approaches – albeit no fault of the authors. A re-analysis of Pawpaw genomics and morphological characteristics over many cultivars (100+) is certainly in order. Hopefully the current revolution in long-read sequencing technology will provide cost-effective means of analysis in the future.

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