Image-based morphometric analysis reveals moderate to highly heritable nut shape traits in pecan

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Abstract Nut shape is an important trait in determining the value of a pecan (Carya illinoensis) nut crop. Nut shape influences attractiveness to consumers, nut filling, ease of mechanical cracking, and is distinctive enough that it is the primary means of cultivar identification. Narrow sense heritability ($h^2$) of a trait is the fraction of phenotypic variance attributed to variation in genes with additive effect. Estimation of $h^2$ is key to breeding programs as it determines the method of selection and amount of genetic gain in each breeding cycle. In the present study, we estimated the heritability of pecan nut shape characters following two different approaches. First, image-based phenotypes of pecan nuts from 34 full-sib families generated from random crosses between 31 different parents were generated and analyzed for 10 different morphometric traits using the computer program Tomato Analyzer. The narrow-sense heritability for each trait was estimated using the mid-parent offspring regression method. Second, a separate set of 19 pecan genotypes were phenotyped for the same shape traits for two years and heritabilities were estimated by variance component analysis. Heritability estimates ranged from 0.41 to 0.83 for the mid-parent offspring regression method and from 0.26 to 0.78 for variance component method. Additionally, elliptical Fourier transform was performed to study the overall variation in nut shape. The first three principal components obtained from Elliptical Fourier transform explained 65.9% of the total variation in shape attributed to the nut's roundness and angularity of proximal and distal ends. The use of the image-based high-throughput method of phenotyping and the heritability estimates obtained in this study directly benefit pecan breeding programs focusing on nut shape traits.

Keywords Breeding · Elliptical Fourier transform · Heritability · Image analysis

Introduction

Pecan belongs to the Juglandaceae (walnut) family and Carya (hickory) genus, which consists of twenty species (Thompson and Conner 2012). Pecan is the most important native North American tree nut species and is endemic to the Mississippi River
watershed and its surroundings. Nut shape is an important trait in determining the value of a pecan nut crop (Grauke and Thompson 1996). Consumers prefer blocky nuts due to an historical association between high-quality kernels and cultivars with a blocky shape (Sparks 1992). Nut elongation affects the kernel quality as highly elongated nuts, especially when they are large, tend to be filled poorly with the kernel tips commonly shrunken (Sparks 1992). Nut shape also determines the ease of mechanical cracking and shelling. Moderately elongated nuts are easier to crack mechanically than are round nuts since round nuts can fall crosswise into the cracker, resulting in damaged nutmeats (Romberg 1968). Alternatively, very long nuts are difficult to crack and shell without breaking the kernel in half. Nuts with a blocky shape, falling between these two extremes, generally produce better filled kernel halves that are more easily separated from the shell in complete halves. Pecan nut shape is distinctive and commonly used as the primary tool in cultivar identification. Pecan nut shape is a combined effect of variation in general nut shape and the angles of the base and apex (Sparks 1992). The variability and stability of these traits makes nut shape an important tool in cultivar identification.

Morphologically, the nut suture divides pecan nut into two symmetric halves. The suture side is exposed when the suture faces up when placing the nuts longest side horizontally, and the non-suture side is exposed when the suture faces laterally. Pecan nuts have been broadly classified by their basic shape, as viewed from the suture side of the nut, ranging from round to elliptic (Sparks 1992; Thompson and Grauke 2003). Pecan nut base and apex shapes also vary and range from round to acuminate. While nut shape has broadly been defined from a cultivar characteristic standpoint, systematic evaluation of pecan nut shape using advanced morphometric methods is lacking.

Common fruit shape measurements include height, width, area, perimeter, volume, and shape indices such as aspect ratio, circularity, rectangularity, blockiness, and proximal and distal angles. Although very useful, these measurements embody a significant number of shortcomings, especially when dealing with complex biological shapes which are not easily measured with linear scales, and the techniques may not optimally capture shape variation. Outline methods such as elliptical Fourier transforms (EFT) (Giardina and Kuhl 1977; Kuhl and Giardina 1982) have been used frequently in plant biology and archaeobotany to understand the overall variation in shape and its covariation with others traits. EFT converts outlines (x,y coordinates) of any shape into a harmonic sum of trigonometric functions, which coefficients can directly be used as shape descriptors (Ferson et al. 1985; Kuhl and Giardina 1982; Lestrel 1997) to perform multivariate analyses such as principal component analysis (PCA). EFT has been used in fruit and leaf shape analysis in a wide range of agricultural species, such as walnut (Demir et al. 2018), apple (Currie et al. 2000; Migicovsky et al. 2018), grapes (Chitwood et al. 2014; Bonhomme et al. 2020, 2021), cherry (Sayinci et al. 2015), tomato (Gonzalo et al. 2009; Visa et al. 2014), hazelnut (Menesatti et al. 2008), olive (Terral et al. 2021), cereals (Bonhomme et al. 2017), pulse (Tarongi et al. 2021) and sweet orange (Costa et al. 2009). Digital shape analysis tools have recently been created to facilitate the acquisition of numerous shape parameters. One useful platform is Tomato Analyzer (TA) which has been formatted to assist in the measurement of shape and color attributes of tomatoes and other fruits (Gonzalo et al. 2009). The morphometric analysis feature built into TA also extracts up to 200 morphometric coordinates along the boundary of the test object which can be used to perform EFT.

Despite its importance, a fundamental understanding of the genetic basis of nut shape in pecan is lacking. Heritability of a trait, for example, provides essential information on the contribution of genotype to the total variation observed for the trait of interest and guides the choice of appropriate selection and breeding methods. Perennial trees species such as pecan, where it is difficult and time-consuming to generate populations for genetic studies, often make use of multiple full-sib families from the breeding program to provide heritability estimates (Hansche et al. 1972a, b). The slope obtained by regressing family means to the corresponding mid-parent phenotypic value gives an estimate of narrow-sense heritability in a method widely known as mid-parent offspring regression (Falconer 1981). Here, we collected image-based phenotypes of various nut shape traits from parents and the offspring of 34 full-sib families and applied the mid-parent offspring regression method to estimate narrow-sense heritabilities. To provide a second heritability estimate of these traits, nut samples from a set of 19 pecan cultivars were
phenotyped for two consecutive years, and variance component analysis was performed to estimate the nut shape heritability, and the two different methods were compared and discussed.

**Materials and methods**

**Plant materials**

The parents used in the mid-parent offspring regression study consisted of named cultivars and selections from pecan breeding programs in the United States. Thirty-one parents were crossed to generate thirty-four full-sib families consisting of 2 to 63 trees per family (Table 1). Since these crosses were originally designed to meet the various objectives of the breeding program, no specific mating design was followed. Offspring were planted at a spacing of 3 m between seedlings in the row and 4.6 m between rows. Seedlings and their parents were grown on an experimental farm located in Tift Co., USA (lat. 31°30'34.74"N, long. 83°38'25.91"W). Seedlings were drip irrigated and nitrogen was applied annually at 112 kg·ha⁻¹, while other nutrients and lime were applied according to leaf or soil analysis. Trees received minimal pesticide applications usually limited to two insecticide and fungicide sprays in August to control hickory shuckworm (*Cydia caryan*) and downy spot (*Mycosphaerella caryigena*), respectively. Progenies were chosen for inclusion in the study based on the presence of fruiting seedlings and the availability of fruit on both parents in 2020.

The variance component analysis heritability study made use of pecan clones that were being evaluated in a commercial yield trial located on the farm listed above. This study included 19 pecan cultivars and selections. Trees for the yield trial were planted into a single orchard block with a tree spacing of 12.2 m x 12.2 m (67 trees·ha⁻¹) and a completely randomized cultivar location. Nitrogen was applied annually at 112 kg·ha⁻¹, while other nutrients and lime were applied according to leaf or soil analysis. Irrigation was used with one 76 L·h⁻¹ microsprinkler per tree. Fungicides and insecticides were applied following Georgia Extension Service recommendations (Hudson et al. 2006). Each cultivar was replicated three to ten times (trees) via grafting onto seedling rootstocks (Table S1). A sample of twenty nuts were collected from each tree in 2015 and 2016 for analysis at which time these trees were six to ten years of age.

**Image acquisition and processing**

Two-dimensional photographs of nuts were taken with a digital camera with the nut’s suture side facing the camera. The camera was set up on the adjustable

| Seed parent | Pollen parent | No. of progeny evaluated |
|-------------|---------------|-------------------------|
| Pawnee      | Elliott       | 63                      |
| Nacono      | Excel         | 24                      |
| Pawnee      | Amling        | 24                      |
| Leger-1     | Amling        | 22                      |
| Faircloth   | Ga-99-2-108   | 21                      |
| Kanza       | Byrd          | 20                      |
| Byrd        | Mandan        | 17                      |
| Amling      | Excel         | 16                      |
| Barton      | Jackson       | 16                      |
| McMillan    | Byrd          | 16                      |
| Carlson Center | Byrd     | 15                      |
| Sumner      | Elliott       | 15                      |
| Syrup Mill  | Ga-99-2-108   | 14                      |
| Excel       | 86-3-32       | 12                      |
| Zinner      | Excel         | 10                      |
| Lucas       | Byrd          | 8                       |
| Maramec     | 99-9-3        | 7                       |
| Pawnee      | Avalon        | 7                       |
| 78-15-51    | Excel         | 6                       |
| Caddo       | Byrd          | 6                       |
| Faircloth   | Byrd          | 6                       |
| Kanza       | 70-6-15       | 6                       |
| Lucas       | Pawnee        | 6                       |
| Pawnee      | Kanza         | 6                       |
| 70-6-15     | Excel         | 5                       |
| Nacono      | Faircloth     | 4                       |
| Zinner      | Byrd          | 4                       |
| 99-12-20    | Lakota        | 3                       |
| Caddo       | Cape Fear     | 3                       |
| 70-6-15     | Pawnee        | 2                       |
| 99-10-3     | Pawnee        | 2                       |
| Kanza       | Excel         | 2                       |
| Oconee      | Excel         | 2                       |

**Total** 390
stand, and nuts samples were laid out horizontally on a light box. A U.S. quarter dollar coin (diameter = 2.43 cm) was used as a scale for each photograph. The raw images were first adjusted for the brightness and contrast so that each nuts image would have black color in white background (BW image), using the batch function implemented in ImageJ 1.52a (Schneider et al. 2012). The BW images were then color inverted to make images readable to TA. The macros used to batch process all the images at once are available at (https://github.com/gitgaurab/pecanmorphometrics). The processed images were then analyzed in Tomato Analyzer 4.0 for 10 shape traits (Fig. 1). Each nut was carefully examined for the boundary line and appropriate marker placement at proximal and distal ends and were corrected if needed. Full description of these shape traits is available in TA 4.0 manual.

Heritability estimation

For mid-parent offspring regression heritability analysis, traits values obtained from TA were averaged across a random sample of ten nuts from each tree. Family means and mid-parent value (average trait value of the parents from each family) were then calculated. Family means were regressed over corresponding mid-parent value by fitting linear regression model (‘lm’) in R (R core team 2021), and t-statistics and probability value (p) were obtained using ‘summary’ function. Slope estimates of the best fitting regression line were obtained for each trait.

For variance component heritability estimation, analysis of variance was performed for the two years (2015 and 2016) of phenotypic data collected using TA from 95 trees of 19 different pecan clones (Table S1). Effect of the genotype, year, and interaction between genotype and year were considered as random effects, and a linear model was fitted in Minitab Version 20.3.0 as:

\[ P_{ij} = \mu + Y_i + g_j + e_{ij}. \]

where, \( P_{ij} \) is the observed phenotype of the \( j \)th genotype in the \( i \)th year; \( \mu \) is the overall mean value of the trait; \( Y_i \) is the random effect of the \( i \)th year, \( g_j \) is the random effect of the \( j \)th genotype, and \( e_{ij} \) is the residuals of the model. The variance component accounted by each term in the model were extracted and broad-sense heritability of the trait was estimated as:

![Geometric diagram of the shape traits analyzed with Tomato Analyzer and their abbreviation. Full explanation of the traits and their derivation is found in the Tomato Analyzer 4.0 manual](image-url)
Heritability \( (H^2) = \frac{\sigma^2_G}{\sigma^2_P} \)

where, \( \sigma^2_G \) is the genotypic effect variance and \( \sigma^2_P \) is the total phenotypic variance.

Elliptical Fourier transforms

Two hundred morphometric points (\( x, y \) coordinates) equally space along the outline curvilinear abscissa were retrieved for each nut from the full-sib families using TA. These coordinates were then read into Momocs v3.0 (Bonhomme et al. 2014) in R to calculate elliptical Fourier coefficients. The number of harmonics was chosen so that it gathers 99% of the harmonic power. Each harmonic is defined by four coefficients (A and B for \( x \); C and D for \( y \) coordinates); the B and C harmonics were zeroed to eliminate asymmetrical variation in nut shape (Iwata et al. 1998). Elliptical Fourier coefficients were averaged across the nuts from an individual tree, and principal component analysis (PCA) was performed using ‘prcomp’ function in R. The minimum and maximum values from first three (see Results) PCs were obtained and used to visualize the corresponding nut sample. Pearson correlation coefficients between the first three PC values and the shape traits that were obtained from TA were examined using ‘cor’ function to understand the possible causes of variation in nut shape. R codes used in performing these analyses are available in https://github.com/gitgaurab/pecanmorphometrics.

Results

Heritability estimates

Slope estimates of the fitted regression line between progeny mean and mid-parent value showed moderate to high narrow-sense heritability for the shape traits measured with TA (Fig. 2). Maximum width and distal angle (macro) showed highest (0.83) and lowest (0.41) narrow-sense heritability, respectively. Heritability of most other traits were greater than 0.5, indicating a larger proportion of variability in these nut shape traits due to the genetic makeup of the pecan trees.

Heritability estimated from the analysis of variance components also showed moderate to high heritability ranging from 0.26 (maximum height) to 0.78 (rectangularity) (Fig. 2). Except the heritability estimates for fruit maximum height and maximum width, traits showed relatively consistent heritability estimates from both methods.

EFT elucidates components of the overall variation in nut shape

The first three PCs obtained from EFT accounted for 65.9% of phenotypic variation in pecan nut shape. The first PC (PC1) explained variation (27.1%) due to the nut’s roundness (Fig. 3). Similarly, second and third PCs (PC2 and PC3) showed shape differences due to the nut’s flatness at the proximal and distal ends (proximal and distal angles) and explained 21.1 and 17.7% of phenotypic variation, respectively. An offspring from a cross between ‘Barton’ and ‘Jackson’ was most rounded, while an offspring from a cross between ‘Kanza’ and ‘Byrd’ were most elliptical. Nut base (proximal angle) shape varied from nearly flat in a ‘Pawnee’ × ‘Elliott’ offspring to acuminate in a ‘Maramec’ × ‘99-9-3’ seedling. Similarly, distal end angle ranged from obtuse in a ‘Leger-1’ × ‘Amling’ offspring to acuminate in a ‘McMillan’ × ‘Byrd’ offspring.

Both parents and offspring used for mid-parent offspring regression heritability estimation showed variation for the shape traits obtained from tomato analyzer (Fig. S1, S2, Table S2). For parents, maximum height ranged from 3.3 to 5.6 cm, width from 1.7 to 2.7 cm, proximal angle from 74° to 133°, distal angle from 69° to 127°, proximal and distal fruit blockiness from 0.35 to 0.68 and 0.29 to 0.59, respectively. Similarly, nut circularity ranged from 0.75 to 0.92, rectangularity from 0.40 to 0.92, rectangularity from 0.40 to 0.53, fruit shape index from 1.4 to 2.5, and ovoidness from 0.01 to 0.29. All the traits we measured in this study, in general, followed a normal distribution in the progenies (Fig. S2). We also observed transgressive segregation for most of the traits (mean phenotypic value for progeny tree being smaller or greater than the mean phenotypic value of parents). The presence of this inheritance pattern can be very important from a breeding perspective if
an objective is to generate progeny with a trait value higher or lower than their parents.

Correlation between PCs obtained from EFT and shape traits from TA showed factors linked with overall variation in nut shape in pecan (Fig. 4). PC1 showed a strong negative correlation ($r = -0.55$, $P < 10^{-16}$) with external fruit shape index (FSIEI), the ratio of nut’s maximum height and maximum width. Similarly, PC1 was positively correlated with distal fruit blockiness ($r=0.65$, $P < 10^{-16}$) and distal angle (macro) ($r=0.90$, $P < 10^{-16}$) indicating variation in nut roundness is strongly affected by nut blockiness and angularity towards the distal end. Nut roundness was also positively correlated to nut’s circularity ($r=0.5$, $P < 10^{-16}$). Correlation analysis also showed that the linear measurements such as height and width alone could not capture the overall variation in nut shape in pecan as indicated by their relatively small correlation with all three PCs. PC2 was negatively correlated with proximal fruit blockiness ($r = -0.56$, $P < 10^{-16}$), circularity ($r = -0.48$, $P < 10^{-16}$), proximal angle ($r = -0.65$, $P < 10^{-16}$), and ovoid index ($r = -0.66$, $P < 10^{-16}$) and positively correlated with the distal fruit blockiness ($r=0.62$, $P < 10^{-16}$), indicating shape variation explained by this PC is likely due to both nut blockiness and angularity. Although not very strong, PC3 generally showed correlation to the traits opposite to that of the correlation shown by PC2 indicating PC2 and PC3 explain variation in nut blockiness and angularity in the opposite direction.
Discussion

Likely due to the difficulty of growing large progenies for genetic studies, very few estimates of the heritability of breeding-related traits in nut crops have been published. Thompson and Baker (1993) applied the mid-parent offspring regression method to estimate narrow-sense heritability of nut weight, nut buoyancy, nut volume, nut density, kernel weight, and percentage kernel in pecan using 152 families collected over 25 years. These traits showed low to moderate heritability ranging from 0.03 (nut density) to 0.38 (kernel weight), indicating these traits are largely affected by the varying crop load due to alternate bearing and environmental factors. Hansche et al. (1972b) estimated the heritability of 18 different traits in walnut by the mid-parent offspring regression method after adjustment for the effect of environment over 14 years. These traits showed low to moderate heritability ranging from 0.03 (nut density) to 0.38 (kernel weight), indicating these traits are largely affected by the varying crop load due to alternate bearing and environmental factors. Hansche et al. (1972b) estimated the heritability of 18 different traits in walnut by the mid-parent offspring regression method after adjustment for the effect of environment over 14 years. These traits included fruit size and shape related traits such as nut length, suture diameter, cheek diameter, and nut weight. They reported a very high narrow sense heritability for these traits: 0.91 for nut length, 0.82 for suture diameter, 0.89 for cheek diameter, and 0.97 for nut weight showing very small effect of environment on these traits. Mehlenbacher et al. (1993) reported low (0.15) to high (0.84) estimates of heritability of various
traits related to nut and kernel defects in hazelnut using mid-parent offspring regression. Traits analyzed included frequency of blanks, moldy kernels, kernels with black tip, doubles, shriveled kernels, poorly filled nuts, and brown stain. Heritability of shape-related traits in pecan has not previously been explored.

One of the limitations of our study was the population of parents selected to study heritability. Heritability is usually estimated with respect to the overall breeding population from which parents should be randomly selected (Hallauer and Miranda 1981). We selected the parents from the population of cultivars (or selections) that were deliberately used or obtained from pecan breeding programs in the United States. This set of parent cultivars were selected for a variety of traits of interest to the breeding program and not exclusively for nut shape traits. However, the variability between these genotypes for the nuts shape traits can justify the methods applied in this study.

TA is designed to provide analysis of slices of tomatoes, peppers, leaves, and seeds. Version 4.0 has been modified to work better with asymmetric (curved) image slices (for example, curvy tomatoes and peppers), and hollow peppers. So, several traits analyzed by the software such as shoulder height and curved fruit shape index are not relevant to the external shape of symmetrical pecan nuts. These traits, along with redundant traits (such as width maximum height, height maximum width, fruit shape index external II, fruit shape index internal I) and traits that cannot be correctly estimated due to pecan’s physical (mechanical) deformities (especially towards the end (proximal angle micro and distal angle micro) were not considered in the analysis. Overall, despite the program having been designed for processing fleshy fruit samples, image analysis of pecan shape was relatively straightforward.

Heritabilities estimated from parent-offspring regression were higher for size-based traits (maximum width and maximum height) than those estimated from variance component analysis. A reason for such variation is a bias of the mid-parent offspring method as it does not consider the effect of year. Size-based traits in pecan vary year to year, reducing heritability estimated from variance components analysis. Pecan is an irregular bearing crop and crop load can affect the nut size associated parameters such as nut width, nut height and correlated traits. Similarly, diseases like pecan scab (Venturia effusa) can also affect nut development and shape and scab infection varies according to summer rainfall patterns (Sanderlin 1994). Heritabilities estimated from variance component analysis for all other shape-related traits were generally higher than those estimated from the mid-parent offspring method in our study. The reason for such disparity is likely due to components of genotypic variance accounted by the two methods: broad sense heritability estimated from variance components accounts for the entire genotypic variance while narrow-sense heritability estimated from mid-parent offspring regressions only includes the additive component of genotypic variance.

Shape-based traits such as rectangularity, fruit blockiness, angle of proximal and distal ends, and degree of ovoid showed high heritability using both estimation methods, indicating the smaller effect of year in these traits. There are no reports of heritability estimates for these traits in other nut crops, but moderate to high heritability estimates have generally been reported in the literature for fruit-shape traits. White et al. (2000) reported heritability estimates for shape indices in pear with variance component analysis of 0.68 for height:maximum width, 0.47 for height of maximum width:height, and 0.47 for width at 25% height:width at 75% height. Similarly, in almond, Martínez-Garcia et al. (2019) reported a heritability estimate of 0.80 for shell length, 0.76 for roundness, but only 0.12 for shell width. Heritability estimated by Zingaretti et al. (2021) in strawberry for additive and dominance variance components of shape traits such as height, width, the ratio between height and width, and circularity were all below 0.4 and the sum of both components ranged between 0.4 and 0.6. Arias-Calderón et al. (2014) have reported very high narrow-sense heritability for the circularity trait in olive fruits (0.93) obtained from variance component analysis using full sib-families from open pollination of 17 olive cultivars. Variance component analysis using forty-four vintage tomato varieties has also shown larger broad-sense heritability of 0.875 ± 0.21, 0.939 ± 0.21, 0.965 ± 0.21, and 0.947 ± 0.22 for rectangularity, proximal angle (macro), distal angle (macro), and degree of ovoid, respectively (Panthee et al. 2013), suggesting that the shape indices can be used as reliable trait parameters in a breeding program. Differences in the genetic background of the
crop, the method used, and the sample size can result in differences in estimates of heritability.

EFT has been used in nut and fruit crops primarily for shape discrimination of genotypes. In almond, the first three PCs obtained from EFT of 699 nut sample outlines captured 85.7% of the total variation in shape on its suture orientation (Demir et al. 2019). Using shape descriptors obtained from EFT, the method was able to correctly identify the original group identity of seven almond cultivars with 94% of accuracy. A very similar result was obtained for 18 almond cultivars by Antonucci et al. (2012) with more than 89% correctly classified. We also estimated the heritability for the first three principal components obtained from EF descriptors using mid-parent offspring regression. All three PCs showed moderate to high heritability (PC1 = 0.40, PC2 = 0.52 and PC3 = 0.78). Zingaretti et al. (2021) obtained a similar result in strawberries, with overall heritability of PC2 greater than PC1 (heritability of PC3 was not calculated). A similar study has been done for apple fruit shape by Currie et al. (2000). The first three PCs in this study had narrow-sense heritability of 0.79, 0.06, and 0.38, respectively. They also reported 90.6% of cumulative phenotypic variability explained by the first three EF PCs. Though different, this is comparable to the percentage of cumulative variance explained by the first three PCs in our study (65.9%). Such differences are likely due to the structural difference in fruit shape between pecan and other fruits studied, and difference in the populations employed in estimating heritability. Given the large variability of nut shape traits in pecan and the moderate to high heritability estimates exhibited by the first three PCs of multivariate analysis, EFT has good potential to be used in the breeding program for nut shape phenotyping and shape-based cultivar identification.

Pecan nut shape is of great interest to the producer and consumer, and therefore the breeder. Pecan nuts are generally sold in lots of a single cultivar to facilitate setting cracking and shelling equipment parameters to maximize complete shell removal with minimal kernel damage. However, the production of large acreages of single cultivars has facilitated the development and spread of more virulent races of pecan scab. Breeding programs are now interested in developing cultivar mixtures capable of producing nuts with similar appearance and shelling characteristics, but with differing resistance genes to mimic the variability found in native groves to reduce the buildup of disease inoculum (Conner and Stevenson 2004).

In the past, most selection pressure has been towards oblong nuts and away from the more round and elongated nut shapes (Grauke and Thompson 1996). Discrimination against these shapes tends to be stronger as nut size increases, because large round nuts often produce an unattractive cupping on the underside of the kernel and large elongated nuts are often poorly filled on the kernel ends. Since large-sized nuts are currently more valuable in the marketplace (Conner and Wells 2015; Sparks 1992), nut shape has become an important factor in the potential value of a new cultivar. In addition to overall shape, shelling of the nuts is enhanced with rounded as opposed to more angular nut base and apex (Romberg 1968). Using these attributes as a guide, breeding program would be selecting for larger ProAMa, DisAMa, PFB, DFB, and rect. Positive correlations amongst many of these traits and relatively high heritability estimates suggest that breeding for overall desirable shapes will be successful.

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Author contributions GB and PC wrote the manuscript with contribution from VB. GB conducted the phenotyping, shape measurement in Tomato Analyzer and performed statistical analysis. GB and VB conducted the morphometric analysis. PC designed the experiment.

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Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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References

Antonucci F, Costa C, Pallottino F, Paglia G, Rimatori V, De Giorgio D, Menesatti P (2012) Quantitative method for shape description of almond cultivars (Prunus amygdalus Batch). Food Bioprocess Tech 5:768–785. https://doi.org/10.1007/s11947-010-0389-2

Arias-Calderon R, Rouiss H, Rodriguez-Jurado D, de la Rosa R, Leon L (2014) Variability and heritability of fruit characters in olive progenies from open-pollination. Sci Hortic-Amsterdam 169:94–98. https://doi.org/10.1016/j.scienta.2014.02.011

Bonhomme V et al (2017) Identification of inter- and intra-species variation in cereal grains through geometric morphometric analysis, and its resilience under experimental charring. J Archael Sci 86:60–67. https://doi.org/10.1016/j.jas.2017.09.010

Bonhomme V, Picq S, Gaucherel C, Claude J (2014) Mocmomcs: Outline Analysis Using R. J Stat Software 56:1–24. https://doi.org/10.18637/jss.v056.i13

Bonhomme V, Picq S, Ivorra S, Evin A, Pastor T et al (2020) Eco-evo-devo implications and archaeobiological perspectives of trait covariance in fruits of wild and domesticated grapevines. PLoS ONE 15:e0239863. https://doi.org/10.1371/journal.pone.0239863

Bonhomme V, Ivorra S, Lacombe T et al (2021) Pip shape echoes grapevine domestication history. Sci Rep 11:21381. https://doi.org/10.1038/s41598-021-00877-4

Chitwood DH, Ranjan A, Martinez CC, Headland LR, Thiem T, Kumar R et al (2014) A modern ampelography: a genetic basis for leaf shape and venation patterning in grape. Plant Physiol 164:259–272. https://doi.org/10.1104/pp.113.229708

Conner PJ, Stevenson KL (2004) Pathogenic variation of Cladosporium caryigenum isolates and corresponding differential resistance in pecan. HortScience 39(3):553–557

Conner P, Wells L (2015) Pecan varieties for Georgia orchards. In: Wells L (ed) Southeastern pecan growers’ handbook. Univ. of Ga. Cooper. Ext. Bull. 1327, pp:27–50

Costa C, Menesatti P, Paglia G, Pallottino F, Aguzzo J et al (2009) Quantitative evaluation of Tarocco sweet orange fruit shape using optoelectronic elliptic Fourier based analysis. Postharvest Biol Tec 54:38–47. https://doi.org/10.1016/j.postharbio.2009.05.001

Currie AJ, Ganeshanandam S, Noiton DA, Garrick D, Sholbourne CJA, Oraguzie N (2000) Quantitative evaluation of apple (Malus x domestica Borkh.) fruit shape by principal component analysis of Fourier descriptors. Euphytica 111:221–227. https://doi.org/10.1023/A:100386255814

Demir B, Sayinci B, Cetin N, Yaman M, Comlek R, Aydin Y, Sutyemce M (2018) Elliptic Fourier based analysis and multivariate approaches for size and shape distinctions of walnut (Juglans regia L.) cultivars. Grasas Aceites 69(4). https://doi.org/10.3989/gya.0104181

Demir B, Sayinci B, Cetin N, Yaman M, Comlek R (2019) Shape discrimination of almond cultivars by elliptic fourier descriptors. Erwerbs-Obstbau 61:245–256. https://doi.org/10.1007/s13041-019-00423-7

Falconer DS (1981) Introduction to quantitative genetics. 2nd Edition. Longman House, U. K

Ferson S, Rohlf FJ, Koehn RK (1985) Measuring shape variation of two-dimensional outlines. Syst Zool 34:59–68. https://doi.org/10.2307/2413345

Giardina CR, Kuhl FP (1977) Accuracy of curve approximation by harmonically related vectors with elliptical loci. Comput Graph Image Process 6:277–285

Gonzalo MJ, Brewer MT, Anderson C, Sullivan D, Gray S, van der Knaap E (2009) Tomato fruit shape analysis using morphometric and morphology attributes implemented in tomato analyzer software program. J Am Soc Hort Sci 134:77–87. https://doi.org/10.21273/Jashs.134.1.77

Grauke LJ, Thompson TE (1996) Pecans and hickories. In: Janick J, Moore JN (eds) Fruit breeding volume&nbsp;III. Nuts. John Wiley & Sons, New York, pp 185–239

Hallauer AR, Miranda FO (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames, U.S.A.

Hansche PE, Beres V, Forde HI (1972) Estimates of quantitative genetic properties of walnut and their implications for cultivar improvement. J Am Soc Hort Sci 97:279–285

Hansche PE, Beres V, Hesse CO (1972) Estimates of genetic and environmental effects on several traits in peach. J Am Soc Hort Sci 97:76–79

Hudson W, Brock J, Culpepper S, Wells L (2006) Georgia pecan pest management guide. Univ of Georgia College of Agr Bul 841

Iwata H, Niikura S, Matsuura S, Takano Y, Ukiay Y (1998) Evaluation of variation of root shape of Japanese radish (Raphanus sativus L.) based on image analysis using elliptic Fourier descriptors. Euphytica 102:143–149

Kuhl FP, Giardina CR (1982) Elliptic Fourier descriptors of a closed contour. Comput Graph Image Process 18:236–258. https://doi.org/10.1016/0146-664x(82)90034-X

Lestrel PE (1997) Fourier descriptors and their applications in biology. Cambridge University Press, Cambridge, U.K.; New York

Martinez-Garcia PJ, Rubio M, Cremades T, Dicenta F (2019) Inheritance of shell and kernel shape in almond (Prunus dulcis). Sci Hortic-Amsterdam 244:330–338. https://doi.org/10.1016/j.scientia.2018.09.041

Mehlenbacher SA, Smith DC, Brenner LK (1993) Variance components and heritability of nut and kernel defects in hazelnut. Plant Breed 110(2):144–152

Menesatti P, Costa C, Paglia G, Pallottino F, D’Andrea S, Rimatori V, Aguzzo J (2008) Shape-based methodology for multivariate discrimination among Italian hazelnut cultivars. Biosyst Eng 101:417–424. https://doi.org/10.1016/j.biosystemseng.2008.09.013

Micgicovsz Y, Li M, Chitwood DH, Myles S (2018) Morphometrics Reveals Complex and Heritable Apple Leaf Shapes. Front Plant Sci 8. https://doi.org/10.3389/fpls.2017.02185
Minitab LLC (2021) Minitab. Retrieved from https://www.minitab.com

Panthée DR, Labate JA, McGrath MT, Breksp JA, Robertson LD (2013) Genotype and environmental interaction for fruit quality traits in vintage tomato varieties. Euphytica 193:169–182. https://doi.org/10.1007/s10681-013-0895-1

Romberg LD (1968) Pecan varieties in 1968. Proc. Southeastern Pecan Growers Assoc. 61:56–65

Sanderlin RS (1994) Effect of nut scab on pecan yield and quality components. In: Smith MW, Reid W, Wood BW (eds). Sustaining pecan productivity into the 21st century. Proc USDA-ARS 2nd Natl Pecan Wkshp

Sayinci B, Ercisli S, Akbulut M, Savsatli Y, Baykal H (2015) Determination of shape in fruits of cherry laurel (Prunus laurocerasus) accessions by using elliptic Fourier analysis. Acta Sci Pol-Hortorum 14:63–82

Schneider CA, Rasband WS, Elciceki KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Sparks D (1992) Pecan cultivars: the orchard’s foundation. Pecan Production Innovations, Watkinsville, Ga

Toralong M, Bonhomme V, Evin A et al (2021) A new way of seeing pulses: preliminary results of geometric morphometric analyses of Iron Age seeds from the site of La Font de la Canya (Barcelona, Spain). Veget Hist Archaeobot 30:77–87. https://doi.org/10.1007/s00334-020-00801-2

Terral JF et al (2021) The shape diversity of olive stones resulting from domestication and diversification unveils traits of the oldest known 6500-years-old table olives from Hisnuley Carmel Site (Israel). Agronomy 11:2187. https://doi.org/10.3390/agronomy11112187

Thompson TE, Baker JF (1993) Heritability and phenotypic correlations of six pecan nut characteristics. J Am Soc Hortic Sci 118:415–418. https://doi.org/10.21273/JASHS.118.3.415

Thompson TE, Conner PJ (2012) Pecan. Handb Plant Breed 8:771–801. https://doi.org/10.1007/978-1-4419-0763-9_20

Thompson TE, Grauke LJ (2003) Pecan nut and kernel traits are related to shelling efficiency. HortScience 38:586–590. https://doi.org/10.21273/Hortsci.38.4.586

Visa S, Cao CX, Gardener BM, van der Knaap E (2014) Modeling of tomato fruits into nine shape categories using elliptic fourier shape modeling and Bayesian classification of contour morphometric data. Euphytica 200:429–439. https://doi.org/10.1007/s10681-014-1179-0

White AG, Alspach PA, Weskett RH, Brewer LR (2000) Heritability of fruit shape in pears. Euphytica 112:1–7. https://doi.org/10.1023/A:1003761118890

Zingaretti LM, Monfort A, Perez-Enciso M (2021) Automatic Fruit Morphology Phenome and Genetic Analysis: An Application in the Octoploid Strawberry. Plant Phenomics 2021. https://doi.org/10.34133/2021/9812910

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

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