Fruit morphometric diversity, oil content, and fatty acid composition of Acrocomia aculeata (Jacq.) Lodd. ex Mart. across eight sites in Costa Rica

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Research Article

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Abstract

Acrocomia aculeata is an emerging multipurpose oil palm with high potential for food, industrial, and bioenergy applications; however, limited information on the phenotypic and biochemical variation in Mesoamerican germplasm constrains its domestication and utilization. In this study, the fruit morphometrics, biomass partitioning, oil content, and fatty acid composition of the mesocarp and kernel of fruits collected from eight sites in Costa Rica were evaluated. Significant variation was observed among the sites for all the evaluated traits. Abangares and Turrubares showed the highest fruit mass and high biomass values, whereas Nicoya and Cuajiniquil presented lower values for several morphometric and biomass traits. The mesocarp oil content ranged from 11.23% to 35.97%, with the highest value recorded in Paso Real, while the kernel oil content ranged from 38.5% to 55.6%, with Turrubares showing the greatest accumulation. Fatty acid profiles differed markedly between tissues: mesocarp oil was dominated by oleic acid (55–64%), whereas kernel oil was characterized by high lauric acid content (27–35%). Principal component analyses revealed distinct patterns among the sites in terms of fruit size, biomass allocation, oil content, and fatty acid composition. These results demonstrate substantial phenotypic and biochemical diversity within the Costa Rican *A. aculeata* germplasm and suggest that different oil allocation patterns occur between mesocarp and kernel. This variability provides a valuable basis for germplasm selection, conservation, and breeding aimed at developing locally adapted, multipurpose production systems.

Introduction

Acrocomia aculeata is a perennial, oleaginous palm of the Arecaceae family, commonly known as macaw palm, bocaiuva, macaúba, and mbocayá; in Costa Rica, it is known as coyol. It is widely distributed across the Neotropics, from the Caribbean and southern Mexico to Argentina (de Lima et al. 2018). *A. aculeata* thrives at relatively high densities in pastures, semideciduous forests and rocky outcrops (Colombo et al. 2018). Fossil evidence suggests a South American origin, with human-mediated dispersal to Central America (Morcote-Ríos & Bernal 2001), and molecular markers indicate a possible diversity center in southeastern Brazil (Lanes et al. 2015).

Owing to its adaptability to diverse environments, including high precipitation, solar radiation and nutrient-deficient soils, as well as its tolerance to drought periods and absence of significant diseases, it is considered a valuable species for the sustainable production of vegetable oils and biofuels. This makes it a strategic option for diversifying agricultural production and reducing dependence on conventional crops (Montoya et al. 2016, Falasca et al. 2016, Plath et al. 2016). The primary value of *A. aculeata* lies in its oil productivity and quality, as both the pulp and kernel contain high concentrations of fatty acids, making it suitable for various industrial applications (del Río et al. 2016, Aires & de Carvalho, 2023). Its favorable oil composition makes it a promising resource for both biofuel and food production, leading to comparisons with African oil palm (*Elaeis guineensis*) as an alternative oil-producing crop (Evaristo et al. 2016; Plath et al. 2016).

In addition to their nutritional and industrial value, oils and extracts derived from *A. aculeata* have demonstrated antioxidant, antidiabetic, anti-inflammatory, antimicrobial, neuroprotective, and photoprotective properties, highlighting their potential for pharmaceutical and cosmetic applications (da Silva et al. 2019, Baiyeri et al. 2026; Aires and de Carvalho 2023, da Silva et al. 2026). *A. aculeata* is also considered an important feedstock for biodiesel production. Mesocarp oil can be converted into biodiesel that meets international fuel quality standards and exhibits desirable oxidative stability and combustion characteristics (Nascimento et al. 2025; Nunes et al. 2015). Furthermore, the byproducts of the fruit, including the shell and endocarp, have potential applications in thermal energy production and the food industry for both human and animal consumption because of their high fiber and protein contents (Prates-Valério et al. 2019, Madeira et al. 2024).

The full utilization of all the fruit components supports a sustainable production chain, increasing the commercial value of the species (Montoya et al. 2016). Theoretically, the oil yield is estimated to be more than 4 tons per hectare annually with proper agronomic management and the development of high-yield germplasms (Colombo et al. 2018, Pires et al. 2013). These projections depend on the variability of fruit and oil traits. For example, studies have reported mesocarp oil contents ranging from 14.65% to 77.54% and kernel oil contents ranging from 33.24% to 68.9% on a dry basis across different Brazilian populations (Ciconini et al. 2013; da Conceição et al. 2015; Montoya et al. 2016). Additionally, the fatty acid composition varies, with oleic acid predominating in the mesocarp oil (up to 79%), which is beneficial for biodiesel and culinary uses, and lauric acid being most abundant in the kernel oil (up to 47%), which is valuable in cosmetic production (Navarro-Díaz et al. 2013; da Conceição et al. 2015; Lescano et al. 2015; Lieb et al. 2019).

Research has advanced the domestication of *A. aculeata* by characterizing its genetic diversity in terms of its morphological traits (Coser et al. 2016), as well as its oil yield and fatty acid composition (da Silva et al. 2019, Silva et al. 2022). In addition, molecular markers are essential for analyzing the genetic diversity and mating systems of natural populations (Coelho et al. 2018) and germplasm collections (Lanes et al. 2015, Lanes et al. 2016, Mengistu et al. 2016). Notably, these studies, including the most recent biometric characterization (Madeira et al. 2024), have been conducted primarily in Brazil, supporting *A. aculeata* domestication, breeding, and technological development (Colombo et al. 2018).

Research on *A. aculeata* has advanced substantially in Brazil, whereas comparatively few studies have been conducted in Central America. Such research includes the description and quantification of palm fruit mesocarp and exocarp carotenoid and tocopherol contents in Guanacaste Province, Costa Rica (Schex et al. 2018). Lieb et al. (2019) quantified the oil content and characterized the fatty acid profile in the fruit mesocarp and kernels at three stages of maturity. Arnáez-Serrano et al. (2019) described preliminary efforts to use *A. aculeata* intercropped with grass and other oleaginous species. The thermodynamic properties of oil from several oleaginous species, including *A. aculeata*, were tested for its biodiesel production suitability (Alvarado-Montero et al. 2018). The fruit morphology and oil composition of *A. aculeata* were characterized but restricted to three sites in Costa Rica, revealing that phenotypic variability is influenced by environmental factors (Alfaro-Solís et al. 2020). A more comprehensive study in Costa Rica used microsatellite markers across 18 sites to examine the genetic diversity and structure of *A. aculeata* in Costa Rica. This study revealed three main genetic clusters located in the lower-central Pacific, upper northern Pacific, and southeastern Pacific. Relatively uniform and low genetic diversity was found in *A. aculeata* populations across Costa Rica (Navarro-Cascante et al. 2023).

Despite these advances, the characterization of fruit biometric traits, oil content, and fatty acid composition remains limited in Mesoamerica, including Costa Rica. This knowledge gap limits the identification and selection of high-yielding germplasms with desirable fatty acid profiles for diverse applications. Therefore, the present study aims to evaluate the fruit morphometric traits, oil content, and fatty acid composition of *A. aculeata* fruits collected from eight sites in Costa Rica. We hypothesize that populations of *A. aculeata* distributed across different regions of Costa Rica would exhibit significant variation in fruit morphometric traits, biomass, oil content, and fatty acid composition, consistent with geographic differentiation among sites. This work contributes to a more comprehensive understanding of *A. aculeata* diversity in Mesoamerica and provides baseline data to support the development of germplasm conservation and the potential for local breeding programs.

Materials and methods

Plant material and sample collection

The study area comprised eight sampling sites in Costa Rica (Fig. 1): Turrubares (province of San José), Río Negro, Paso Real and Osa Peninsula (province of Puntarenas), Orotina (province of Alajuela), Abangares, Cuajiniquil and Nicoya (province of Guanacaste) (Fig. 1). At each sampling site, three palms were selected, and one fruit bunch was harvested from each palm. For the selection of bunches, fruit maturity was considered on the basis of the characteristics of dark brown coloration (Schex et al. 2018). Each sampling site consisted of areas where mature reproductive trees with relatively dispersed fruits were growing. The minimum distance between trees at each site ranged from approximately 20–100 m, depending on the total number of trees at each site.

Fruit morphometrics

A subsample of eight fruits per bunch was selected for individual measurements of fresh fruit mass, transverse diameter and longitudinal diameter. Each fruit was then separated into the following components: husk (exocarp), pulp (mesocarp), shell (endocarp), and kernel (endosperm). The husk was removed, and the pulp was manually separated using a clean knife until the majority of the pulp was removed. Seeds with residual mesocarps were placed in a beaker containing a 1.5 M sulfuric acid solution maintained at 65°C under constant agitation for 30 min to loosen the remaining pulp. The seeds were rinsed under running water until the residual mesocarp was removed to obtain cleaned seeds. The individual seeds were cracked to separately obtain the shell and the kernel. Finally, each component (husk, pulp, endocarp and kernel) was placed in a drying oven at 60°C. After 72 hours, the dry weights of all the fruit components were recorded.

Determination of oil content

A random subsample of eight fruits per bunch was selected. The pulp and kernels were removed as described above and stored at -80°C for 24 hours. The tissues were protected from light for further freeze-drying for 72 hours. The pulp and kernels were ground separately into a fine powder and analyzed in duplicate to determine the oil content. Approximately three grams of each sample was weighed into glass tubes, and 20 mL of a hexane–dichloromethane mixture (4:1, v/v) was added to dissolve the lipid fraction. The tubes were subjected to ultrasonication for 30 minutes and then centrifuged at 1,500 rcf for 5 minutes. The supernatant was transferred to clean glass tubes and evaporated at 40°C for 24–48 hours to obtain the lipid phase. The oil content was calculated as the gravimetrical difference between the initial dry sample mass and the final mass after complete solvent evaporation.

Determination of Fatty Acid Composition via GC—MS

To determine the fatty acid composition, 0.05 g of each oil extract was esterified by adding 2 mL of 14% boron trifluoride (BF_3) in methanol and 1 mL of toluene. The mixture was vortexed and heated at 100°C for 1 hour. After cooling, water and hexane were added to induce phase separation. The upper organic phase was collected and filtered through a Pasteur pipette packed with a small piece of cotton and a spatula tip of anhydrous sodium sulfate (Na_2SO_4) to remove residual moisture. The dried extract was subsequently transferred to vials for GC analysis.

Fatty acid methyl esters (FAMEs) were analyzed using a gas chromatograph (Thermo Scientific TRACE 1310) equipped with a TraceGOLD TG-5MS column (30 m × 0.25 mm × 0.25 μm) coupled to a mass spectrometer (TSQ 9000). The injector temperature was set to 250°C, with a constant carrier gas flow rate of 1.3 mL/min. The oven was programmed to start at 100°C, increase at 5°C per minute until it reached 285°C (held for 5 minutes), and then increase to a final temperature of 350°C. Fatty acid methyl esters were identified by comparing their retention times and mass spectra with those of a commercial standard mixture, Supelco 37 Component FAME Mix CRM47885 (Supelco), analyzed under the same chromatographic conditions. Fatty acid composition was expressed as the relative percentage of each detected fatty acid with respect to the total FAME peak area.

Statistical analysis

Statistical analyses were performed using Minitab 19 and R. For fruit morphometric and biomass traits, the eight fruits measured from each bunch/palm were considered subsamples and were not treated as independent biological replicates for testing differences among sampling sites. Individual fruit measurements were first averaged at the palm/bunch level, and these palm/bunch-level means were used as biological replicates in the statistical analyses. Therefore, each sampling site was represented by three biological replicates, corresponding to three different palms. One-way analysis of variance (ANOVA) was conducted to evaluate the effect of sampling site on each fruit morphometric, biomass, and oil content trait. When significant differences were detected, Tukey's post hoc test was used for multiple comparisons among sites. For oil content, duplicate determinations were averaged prior to statistical analysis, and palm/bunch values were used for site comparisons. Fatty acid composition was expressed as the relative percentage of total detected fatty acids, and site comparisons were performed using palm per bunch-level values. Principal component analysis (PCA) was performed to explore multivariate patterns among samples based on fruit morphometric traits, biomass partitioning, oil content, and fatty acid composition. For fatty acid composition, PCA was used as an exploratory approach based on relative fatty acid proportions.

Results

Fruit morphometrics and oil content

Significant differences for all the evaluated traits and among the eight sites studied were observed (Table 1). The highest mass of fresh fruits was observed in Abangares (39.43 g) and Turrubares (36.88 g), whereas Cuajiniquil had the lowest fruit mass (26.43 g) as well as Nicoya (26.74 g). Similarly, the highest transverse diameter was observed in Turrubares (40.68 mm) and Abangares (39.87 mm), whereas Cuajiniquil and Nicoya produced smaller fruits. Longitudinal diameters were similar, with higher values in Abangares, Río Negro, and Turrubares and the lowest values in Cuajiniquil. Intermediate values of TD and LD were observed in Orotina, Río Negro, Paso Real, and the Osa Peninsula, which showed overlapping statistical groupings, indicating variation in fruit size across sites.

Differences in fruit biomass partitioning were also observed. Abangares had the highest husk DM dry mass (4.22 g), whereas Nicoya had the lowest value (2.85 g). Pulp DM varied widely among the sites, with the highest values in Paso Real (5.35 g), differing significantly from those in Cuajiniquil and Nicoya, which had the lowest pulp DM (2.75 g and 2.53 g, respectively). With respect to shell dry mass, a similar behavior to that of pulp DM was observed, with Paso Real exhibiting the highest value, which was significantly different from that of Nicoya and Cuajiniquil, whose values were also the lowest. The highest kernel DM was also recorded in Paso Real (2.47 g), Turrubares (2.48 g) and Abangares (2.33 g). Conversely, Orotina, Río Negro, the Osa Peninsula and Nicoya exhibited the lowest and relatively homogeneous values. Cuajiniquil displayed the lowest value for the kernel DM (1.60 g).

Regarding the oil content, significant variation was observed among the sites for both the pulp and the kernel oil contents (Table 1). Paso Real presented the highest pulp oil content (35.97%), which significantly exceeded all the other sites. Notably, the pulp oil content was more than threefold greater than that of Nicoya (11.23%). Paso Real combined the highest pulp dry mass with the highest pulp oil content. Sites such as Abangares, Río Negro, Osa Peninsula and Orotina recorded similar values of pulp oil content, while the lowest values were represented by Nicoya and Turrubares.

On the other hand, the values of the kernel oil content ranged from 38.50% on the Osa Peninsula to 55.60% in Turrubares. Among the sites, Paso Real and Osa Peninsula showed the lowest kernel oil content, while the remaining sites presented intermediate values. The relationship between the oil content of the pulp and that of the kernel exhibited a contrasting pattern. All the sites exhibited higher oil concentrations in the kernel than in the pulp, with some variations in the ratio of pulp to kernel oil. In Turrubares and Nicoya, the kernel oil content was approximately 4.0-fold and 3.7-fold higher than the pulp oil content, respectively. Orotina, Río Negro, Abangares and Osa Peninsula showed similar ratios between 2.3 and 1.8-fold. In contrast, Paso Real showed the lowest difference between pulp and kernel oil content (~ 1.1-fold).

Table 1
Morphometric and oil content traits of *A. aculeata* from eight sites in Costa Rica. The mean values within rows not sharing a common letter are significantly different at $p < 0.05$. Fruit FM: fresh mass of fruits, TD: transverse diameter, LD: longitudinal diameter, DM: dry mass.

Fruit traits	Abangares	Cuajiniquil	Nicoya	Orotina	Osa Peninsula	Paso Real	Río Negro	Turrubares
Morphometrics								
Fruit FM	39.43 ± 4.74 a	26.43 ± 2.48 c	26.74 ± 1.94 c	32.05 ± 3.28 b	31.26 ± 2.22 b	32.25 ± 3.31 b	29.64 ± 3.23 b	36.88 ± 3.52 a
TD (mm)	39.87 ± 1.64 a	35.21 ± 1.35 d	35.83 ± 0.97 cd	37.21 ± 1.82 b	35.99 ± 0.90 bcd	36.42 ± 1.34 bcd	37.00 ± 1.34 bc	40.68 ± 1.86 a
LD (mm)	39.35 ± 2.05 a	35.02 ± 1.30 d	36.27 ± 1.37 cd	37.49 ± 2.47 bc	37.24 ± 1.65 bc	36.77 ± 1.79 cd	38.93 ± 2.64 ab	39.03 ± 2.75 a
Husk DM (g)	4.22 ± 0.42 a	3.47 ± 0.45 bcd	2.85 ± 0.24 e	3.01 ± 1.24 de	3.16 ± 0.37 cde	3.80 ± 0.90 ab	3.65 ± 0.43 abc	2.95 ± 0.60 de
Pulp DM (g)	4.54 ± 1.54 ab	2.75 ± 1.02 c	2.53 ± 0.60 c	4.03 ± 1.22 b	3.86 ± 0.69 b	5.35 ± 1.68 a	4.79 ± 1.05 ab	4.31 ± 1.12 b
Shell DM (g)	7.66 ± 1.00 a	5.25 ± 0.57 b	5.65 ± 0.33 ab	5.55 ± 0.35 ab	5.01 ± 0.46 ab	6.38 ± 0.54 ab	5.68 ± 0.84 ab	6.60 ± 0.68 ab
Kernel DM (g)	2.33 ± 0.29 a	1.60 ± 0.30 c	1.92 ± 0.18 b	1.94 ± 0.26 b	1.99 ± 0.22 b	2.47 ± 0.26 a	2.00 ± 0.41 b	2.48 ± 0.36 a
Oil content								
Pulp (%)	21.99 ± 4.84 c	26.47 ± 1.04 b	11.23 ± 2.92 d	20.13 ± 0.61 c	21.94 ± 1.99 c	35.97 ± 4.52 a	21.16 ± 1.30 c	13.79 ± 3.00 d
Kernel (%)	43.08 ± 2.89 bcd	42.20 ± 3.03 cd	41.56 ± 3.17 d	45.68 ± 3.03 b	38.51 ± 5.03 e	40.77 ± 3.32 de	44.80 ± 2.73 bc	55.60 ± 3.61 a

Principal component analysis of fruit traits and oil content

Principal component analysis (PCA) was performed to visualize the relationships among fruit morphometric traits, biomass partitioning, and oil content across the eight sites (Fig. 2). The first two principal components explained 62.0% of the total variation, with PC1 accounting for 41.4% and PC2 accounting for 20.6%. PC1 was associated mainly with fruit traits related to size and biomass, including FM, LD, TD, kernel DM, shell DM and pulp DM. Sites with larger fruits and greater biomass accumulation, particularly Abangares and Turrubares, were located toward the positive side of PC1. In contrast, Cuajiniquil and Nicoya were distributed mainly on the negative side of this axis because of their smaller fruits and lower biomass values.

PC2 was primarily associated with contrasting oil accumulation patterns between fruit tissues. Pulp oil content and pulp DM mass were associated with the positive side of PC2, whereas the kernel oil content was strongly associated with the negative side of this axis. Paso Real was positioned in the upper region of the biplot, which is consistent with its high pulp dry mass and high pulp oil content. Conversely, Turrubares was located in the lower-right region, related to the high kernel oil content, high kernel DM, and greater fruit size. This PCA supported the results shown in Table 1 and indicated that differentiation among sites was influenced mainly by variations in fruit size, dry biomass allocation, and differences in oil accumulation between the pulp and the kernel.

Fatty acid profile

Fatty acid composition of the kernel

Among the total fatty acids, lauric acid (C12:0) was the most abundant fatty acid in the kernels of the fruits at all the sites studied (Fig. 3). The relative content varied from 27.09 ± 2.01% on the Osa Peninsula to 34.91 ± 1.44% in Río Negro. Turrubares, Río Negro and Abangares presented the highest lauric acid contents, but compared with the other sites, the Osa Peninsula presented significantly lower lauric acid contents. The second most abundant fatty acid was oleic acid (C18:1), whose abundance ranged from 22.01 ± 3.14% in Abangares to 29.33 ± 2.07% in the Osa Peninsula. Because fatty acid values were expressed as relative percentages, samples with higher relative lauric acid content tended to show lower relative oleic acid content. Among saturated medium-chain fatty acids, myristic acid (C14:0) was the third most abundant, with approximately 15–16% of the total fatty acid content. A narrow but significant variation was observed among the sites. Nicoya and Abangares had the highest contents, whereas Cuajiniquil and Río Negro had the lowest values. Caprylic (C8:0) and capric (C10:0) acids were detected at moderate levels (2.4–4.7%). Significant variation was observed, with Río Negro exhibiting the highest concentrations and Osa Peninsula presenting the lowest content.

Palmitic acid (C16:0) was the fourth most abundant fatty acid, ranging from 9.72 ± 0.17% in Río Negro to 12.48 ± 0.29% in the Osa Peninsula. In contrast with lauric acid, palmitic acid levels were significantly higher in the Osa Peninsula than in Río Negro and other sites. Some fatty acids were detected at low to moderate concentrations. Stearic acid (C18:0) varied from 3.97 ± 0.39% in Río Negro to 5.18 ± 0.23% in the Osa Peninsula. Similarly, linoleic acid (C18:2) was a minor but consistent component of the kernel oil, varying between 3.26 ± 0.70% in Abangares and 4.70 ± 0.64% in the Osa Peninsula. Long-chain fatty acids such as arachidic (C20:0) and C20:1 were detected at very low concentrations (< 0.3%) and showed limited variation among the sites.

PCA of kernel fatty acid composition

Principal component analysis (PCA) was used to visualize the variation in kernel oil fatty acid composition among the eight *A. aculeata* sites (Fig. 4). The first two principal components explained 75.5% of the total variation, with PC1 and PC2 accounting for 54.2% and 21.3%, respectively. The biplot revealed a clear contrast along PC1 between medium-chain saturated fatty acids and longer-chain fatty acids. Caprylic (C8:0), capric (C10:0), and lauric (C12:0) acids were strongly associated with the negative side of PC1, whereas palmitic (C16:0), palmitoleic (C16:1), oleic (C18:1), and linoleic (C18:2) acids were associated with the positive side of the axis. This pattern reflected the inverse relationship observed between medium-chain saturated fatty acids and long-chain unsaturated fatty acids. The samples located on the negative side of PC1 were characterized by higher relative contents of C8:0, C10:0, and C12:0, whereas the samples on the positive side were associated with higher proportions of C16:0, C16:1, C18:1, and C18:2. Río Negro was positioned mainly on the negative side of PC1, which is consistent with its higher concentrations of lauric, caprylic, and capric acids and lower proportions of oleic and palmitic acids. In contrast, the Osa Peninsula clearly separated toward the positive side of PC1, demonstrating its distinctive oil kernel profile characterized by lower lauric acid content and higher relative abundance of palmitic, palmitoleic, oleic, and linoleic acids. PC2 contributed to the differentiation of samples according to fatty acids with positive loadings, particularly stearic acid (C18:0), arachidic acid (C20:0), and myristic acid (C14:0). Samples positioned in the upper region of the biplot were therefore associated with higher relative contents of these fatty acids, whereas those in the lower region were more closely related to oleic, linoleic acids and C20:1. This axis contributed to the separation of some samples from Paso Real, Nicoya, and Abangares from those located in the lower portion of the biplot.

The exploratory PCA supported the descriptive patterns observed in the fatty acid profiles and separated samples according to relative differences in kernel oil composition. One group is represented by sites with higher concentrations of medium-chain saturated fatty acids, particularly C8:0, C10:0, and C12:0, and the other is characterized by increased proportions of longer-chain fatty acids, especially C16:0, C16:1, C18:1, and C18:2. The distinct position of the Osa Peninsula supports the existence of a differentiated kernel oil profile within the Costa Rican germplasm analyzed.

Fatty acid composition of the mesocarp

The accumulation of fatty acids in the mesocarp differed from that in the kernel. Oleic acid (C18:1) was highly abundant, with a variation from 55.13 to 63.61% of the total fatty acid content (Fig. 5). The highest content was observed in Cuajiniquil (63.61 ± 3.84%), Osa Peninsula (63.56 ± 8.55%), Nicoya (63.40 ± 1.02%) and Orotina (63.12 ± 5.40%), whereas Río Negro had the lowest content (55.13 ± 3.60%). Palmitic acid (C16:0) was the second most abundant fatty acid, with a relative content ranging from 17.68 ± 1.38% in Turrubares to 22.00 ± 1.18% in Paso Real. Significantly higher concentrations were detected in Paso Real and Río Negro than in Nicoya, the Osa Peninsula, and Turrubares. The content of palmitoleic acid (C16:1) varied across sites nearly fivefold. The highest content was recorded in Río Negro (10.99 ± 3.37%) and Paso Real (9.06 ± 1.30%), whereas Cuajiniquil had the lowest concentration (2.32 ± 0.50%). Similarly, linoleic acid (C18:2) varied significantly from 5.72 ± 2.19% in Cuajiniquil to 12.10 ± 2.70% in Turrubares. The levels differed significantly between Turrubares and Cuajiniquil, Nicoya, and Orotina.

Regarding saturated fatty acids, the content of stearic acid was higher in Cuajiniquil (6.40 ± 1.89%) than in all the other sites, whose values ranged between 1.41% and 2.83%. Other medium-chain saturated fatty acids occurred at low concentrations (< 1.5%) but significantly varied among the sites. Río Negro had the highest content of lauric acid (1.37 ± 0.58%), whereas Orotina and Osa Peninsula had the lowest relative concentrations of this fatty acid (< 0.05%). In addition to myristic acid, the highest concentrations were observed in Río Negro (0.81 ± 0.20%) and Nicoya (0.80 ± 0.20%), whereas Osa Peninsula had significantly lower concentrations (0.10 ± 0.02%). Fatty acids such as caprylic, capric, arachidic, and C20:1 were detected at very low concentrations of less than 0.5% of the total fatty acids.

PCA of mesocarp fatty acid composition

Principal component analysis (PCA) explained 64.9% of the total variation in mesocarp fatty acid composition, with PC1 and PC2 accounting for 37.8% and 27.1% of the variance, respectively (Fig. 6). The distribution of samples and fatty acid vectors supported the differences observed among sites in the individual fatty acid analyses. PC1 was associated mainly with the contrast between oleic acid (C18:1) and the medium-chain saturated fatty acids C8:0, C10:0, C12:0, and C14:0. Positive PC1 scores were related to higher concentrations of medium-chain fatty acids and, to a lesser extent, palmitic acid (C16:0) and palmitoleic acid (C16:1). Negative PC1 scores were associated with higher oleic acid content. Accordingly, Río Negro and Paso Real were positioned toward the positive side of PC1, which is consistent with their higher levels of palmitic and palmitoleic acids. In contrast, the relatively high oleic acid concentrations of the Osa Peninsula, Orotina, Nicoya, and some samples from Turrubares were distributed toward the negative side of PC1. Turrubares had an intermediate position but was more closely associated with linoleic acid (C18:2), in agreement with its significantly higher C18:2 content.

PC2 was influenced primarily by stearic acid (C18:0) and arachidic acid (C20:0) on the positive axis, whereas palmitoleic acid (C16:1) was strongly associated with the negative axis. This separation distinguished Cuajiniquil from most other sites, reflecting its elevated stearic acid content. Conversely, Río Negro and Paso Real were located mainly in the lower-right region of the biplot, which is consistent with their increased concentrations of palmitoleic and palmitic acids. PCA revealed distinct mesocarp oil profiles among the sites. Cuajiniquil was associated mainly with the accumulation of stearic acid. Conversely, Río Negro and Paso Real were located mainly in the lower-right region of the biplot, which is consistent with their increased concentrations of palmitoleic and palmitic acids, whereas Osa Peninsula, Orotina, and Nicoya tend to cluster because of higher oleic acid contents.

Discussion

Fruit morphometrics, dry biomass and oil content

The eight sites of *A. aculeata* sampled in Costa Rica displayed significant variation in fruit morphometrics, dry biomass partitioning and the oil content of the mesocarp and kernel. Significant differences in FM, TD and LD were detected among the sites. Nicoya and Cuajiniquil have relatively small fruits and low dry biomass in both the kernel and mesocarp, while the largest fruits were recorded in Turrubares and Abangares. Paso Real was distinguished by high pulp dry mass and high kernel dry mass, whereas Abangares had the highest husk dry mass, and Turrubares had high kernel DM. The PCA supported these observations, as the first principal component (PC1) was associated with fruit size traits and clearly separated sites with larger fruits (Abangares and Turrubares) from those with smaller fruits (Nicoya and Cuajiniquil). Similar to Alfaro-Solis et al. (2020), the fruit weights ranged between approximately 33 g and 45 g, and the diameters varied between ~ 40 and 45 mm, which indicates that the morphometric variation observed is within the expected range for *A. aculeata* in Costa Rica. Interestingly, the fruit size of Turrubares was comparable to that of El Coyol, whereas the fruits of the Osa Peninsula and Paso Real were smaller than those of La Palma. Both “El Coyol” and “La Palma” are included in the study by Alfaro-Solís et al. (2020) and are geographically close to Turrubares and the Osa Peninsula, respectively. Significant differences among regions in terms of both fruit size and the proportions of fruit components were described by Alfaro-Solís et al. (2020), who reported that both fruit dimensions and dry biomass are site dependent.

The values of fruit fresh mass and diameter observed are also comparable to those reported in Brazilian populations, where fruit mass varies depending on site conditions. Ciconini et al. (2013) reported a fruit mass ranging from 12.7 g to 57.4 g, with variation both within and among sites. Brazilian germplasms of *A. aculeata* have displayed large variations in terms of fruit diameter and dry mass, with distinct population profiles. Large differences in fruit traits and oil yield are characterized especially by differences in the oil content in the mesocarp and total fruit weight (da Conceição et al. 2015, Madeira et al. 2024). Populations in Brazil have greater variation than those in Costa Rica, with fruit diameters ranging from 29 to 59 mm and large differences in the dry mass of the kernel and mesocarp. This suggests that although the germplasm of Costa Rica varies, it does not necessarily represent the full phenotypic diversity of *A. aculeata* (Madeira et al. 2024).

On the other hand, significant differences in biomass partitioning were observed. Sites such as Paso Real presented the highest pulp, shell, and kernel dry masses, whereas Cuajiniquil and Nicoya presented the lowest values. The PCA clearly demonstrated this biomass allocation. Paso Real was associated with high pulp dry mass and pulp oil content, whereas Turrubares was associated with high kernel oil content. This separation along PC2 suggests contrasting oil accumulation patterns between mesocarp and kernel tissues. Similar variation in the proportion of fruit components has been reported previously, with pulp representing approximately 44–49% of the total fruit mass and kernel fractions, while variability in the proportion of kernels (5.9–9.1%) has also been reported (Alfaro-Solís et al. 2020). The high pulp DM values observed in Paso Real are comparable to those reported for the Brazilian germplasm studied by Madeira et al. (2024). These authors also described large variations in kernel dry mass and similar high kernel DM values observed at sites in Costa Rica, which suggest that compared with Brazilian genotypes, the germplasm in Costa Rica has the potential for kernel oil production (Madeira et al. 2024). The variation in shell and husk dry mass across sites suggests that traits related to the structural function of *A. aculeata* are highly variable. Paso Real had high shell DM, whereas Abangares had the highest husk DM. This variability is in line with Alfaro-Solís et al. (2020), who reported significant differences in husk proportion among sites with up to 32% fruit mass. Madeira et al. (2024) similarly demonstrated that variability in husk, pulp, and kernel masses explains a large proportion of the phenotypic divergence among accessions, which supports our observation that differences in dry biomass drive phenotypic diversity and differentiation among sites in *A. aculeata* (Ciconini et al. 2013, da Conceição et al. 2015, Madeira et al. 2024).

Abangares, Orotina, Río Negro, and the Osa Peninsula displayed intermediate pulp oil contents of approximately 21%. Paso Real had the highest content (35.97%), which was significantly different from that at all the other sites. Compared with reports in Costa Rica, these results are consistent with the highest pulp and kernel oil values found in La Palma and La Garita, respectively, both of which are geographically close to Paso Real and Turrubares (Alfaro-Solís et al. 2020). The variation in pulp oil content (11.23–35.97%) is within the broad variability reported in the literature, although it is lower than that reported for some Brazilian populations. Ciconini et al. (2013) reported average pulp oil contents of approximately 25% (dry basis), with relatively small differences among sites, whereas da Conceição et al. (2015) reported even higher values, reaching up to 77% in some genotypes. Madeira et al. (2024) reported high pulp oil content in one accession, whereas the mean values at other sites were comparable to those reported here.

With respect to the kernel oil, Turrubares had the highest oil content (55.60%), while the values across all the sites ranged from 38.5% to 55.6%. The highest kernel oil contents observed in the present study closely resemble those reported by Lieb et al. (2019) for Costa Rican populations, who reported kernel lipid concentrations typically ranging from 54% to 56% and consistently higher than those observed in the mesocarp, whereas Ciconini et al. (2013) reported kernel oil contents reaching 69% in Brazilian germplasms. These results are consistent with previous reports for *A. aculeata*, confirming that the kernel is the main oil accumulation tissue of the fruit. PCA further emphasized these differences in oil accumulation, with PC2 distinguishing sites associated with pulp oil (Paso Real) from those associated with kernel oil accumulation (Turrubares). An important contribution of our work is that the relative ratio between pulp and kernel oil observed is highly variable, suggesting differing accumulation patterns among the germplasms across the sites studied in Costa Rica.

Fatty acid profiles

Fatty acid composition of the kernel

The kernel oil of *A. aculeata* was dominated by medium-chain saturated fatty acids, particularly lauric and myristic acids. Among long-chain fatty acids, oleic acid was the most abundant unsaturated fatty acid. Linoleic acid (C18:2) was present in lower proportions (3.26–4.70%). This profile agrees with reports that *A. aculeata* kernel oil is enriched in medium-chain saturated fatty acids, which is consistent with previous findings in Costa Rican (Lieb et al. 2019; Alfaro-Solís et al. 2020) and Brazilian genotypes (da Conceição et al. 2015, Silva et al. 2022). The lauric acid content (27–35%) was lower than that reported previously in Costa Rican kernels (Lieb et al. 2019, Alfaro-Solís et al. 2020) and was highly similar to that reported in natural populations in Brazil (da Conceição et al. 2015). In contrast, oleic acid (22–29%) overlaps the upper values observed in Costa Rica and some Brazilian germplasms, mainly on the Osa Peninsula, where lauric acid is present in low proportions and oleic acid is present in the highest content (da Conceição et al. 2015, Alfaro-Solís et al. 2020, Vargas-Carpintero et al. 2021).

The oil profile of the eight sites was consistent, with lauric and oleic acids being the two most abundant fatty acids. In agreement with fruit traits and oil content, these differences are likely influenced by environmental and genetic backgrounds. Lieb et al. (2019) demonstrated that kernel fatty acid composition is stable across fruit maturity stages, which suggests that the differences among sites may be associated with environmental conditions and genetic differentiation rather than harvesting time. Additionally, the genetic structure previously described for *A. aculeata* in Costa Rica (Navarro-Cascante et al. 2023) may contribute to these patterns. Populations belonging to different genetic clusters may exhibit distinct fatty acid profiles. The clustering of the Osa Peninsula in the PCA may be related to its genetic similarity with Panamanian populations (Morales-Marroquín et al. 2026).

Fatty acid composition of the mesocarp

The mesocarp oil was characterized by a profile of high levels of oleic acid, which was the predominant fatty acid, followed by palmitic, linoleic, and palmitoleic acids. Across the eight sites, oleic acid ranged from approximately 55% to 64%, while palmitic acid varied from 17.7% to 22.0%. This composition is in agreement with previous reports that *A. aculeata* mesocarp oil is rich in C18:1, with oleic acid concentrations ranging from approximately 48% to 76%, palmitic acid concentrations ranging from 17% to 27%, and linoleic acid ranging from 7% to 20% in Costa Rican and Brazilian populations (da Conceição et al. 2015; Alfaro-Solís et al. 2020; Madeira et al. 2024)

Significant geographic variation was observed among the sites, particularly for palmitoleic, linoleic, and stearic acids. Cuajiniquil displayed a distinctive profile characterized by lower palmitoleic acid and higher stearic acid contents, which was consistent with its separation in the PCA. In contrast, Río Negro and Paso Real were associated with higher palmitic and palmitoleic acid levels, whereas Osa Peninsula, Orotina, and Nicoya were related to higher oleic acid contents. These patterns indicate that although the mesocarp oil profile is generally characterized by high oleic acid content, Costa Rican populations exhibit site-specific variation in fatty acids other than oleic acid. Such variation may reflect the combined influence of environmental conditions and genetic background, as previously suggested for *A. aculeata* populations in Costa Rica and Brazil (Alfaro-Solís et al. 2020; Madeira et al. 2024).

Genetic and environmental factors influencing phenotypic diversity

The phenotypic variability in our study is clearly consistent with the findings of previous studies in Brazil and Costa Rica, which have demonstrated the diversity of this species across environments and populations. This diversity suggests that both specific environmental conditions and genetic differentiation may contribute to the variation observed across sites. In this sense, Alfaro-Solis et al. (2020) reported strong phenotypic differentiation in three regions of Costa Rica influenced by environmental factors such as precipitation and humidity. Precipitation, soil conditions and genetic diversity play major roles in determining variations in oil content and fruit characteristics in Brazil (Ciconini et al. 2013, da Conceição et al. 2015). Vargas-Carpintero et al. (2021) reported that *A. aculeata* exhibits high phenotypic variability across its distribution because of its wide ecological amplitude and adaptation to different edaphoclimatic conditions occurring from semiarid to humid regions, which impose different selective pressures that result in variations in traits such as fruit size, biomass accumulation and oil content.

The variation among sites is consistent with previously reported genetic structuring (Navarro-Cascante et al. 2023), but causal relationships cannot be established without integrated phenotypic and genomic analyses. These authors reported eighteen sites were grouped into three main clusters (A, B and C) that showed moderate to high differentiation among the sites.

In our research, Abangares, Nicoya, Orotina and Turrubares were included in Cluster A (Central and North-lower Pacific), which exhibited significant variation in fruit size and oil content despite their low genetic diversity. Abangares and Turrubares showed the highest fruit mass and high kernel dry mass, whereas Nicoya presented the lowest values for pulp oil. These differences between low genetic diversity and high phenotypic variability suggest that environmental factors that interact with genetic background play important roles in the variation in fruits and oil traits. On the other hand, Paso Real and the Osa Peninsula are in Cluster C (South Pacific) according to Navarro-Cascante et al. (2023). These sites showed the greatest genetic differentiation between Cluster A and Cluster B and formed a clearly separate group. Interestingly, in our study, Paso Real and the Osa Peninsula also demonstrated distinct phenotypic characteristics. The separation of Cluster C was partially explained by geographical isolation and the lower density of individuals (Navarro-Cascante et al. 2023). Additionally, Morales-Marroquín et al. (2026) reported that the population of *A. aculeata* sampled on the Osa Peninsula is clustered with populations from Panama; hence, these individuals have a distinct genetic identity compared to other Costa Rican populations. Genetic continuity between the Mesoamerican and Costa Rican groups was observed but disrupted by a divergent group toward Panama. This genetic distinctiveness suggests historical isolation driven by ecological or geographic barriers near the southern limit of the isthmus (Morales-Marroquín et al. 2026). These patterns are consistent with the hypothesis that both genetic background and local environmental conditions contribute to trait differentiation.

Implications for conservation and breeding strategies

A. aculeata has considerable potential as a multipurpose crop, providing high-quality edible and functional oils, bioactive compounds for cosmetic and pharmaceutical applications, and feedstocks for biofuel production (Giunco et al. 2025). In addition, residues generated during fruit processing can be integrated into biorefinery platforms for the production of bioenergy, biomaterials, and animal feed (Aguilar-Aguilar et al. 2024). Given this potential, a deeper understanding of genetic, phenotypic and biochemical diversity is essential to support effective conservation and breeding strategies. The variability observed within and among populations of *A. aculeata* has been recognized as a key resource for domestication and genetic improvement (Ciconini et al. 2013; da Conceição et al. 2015). Therefore, the characterization of fruit morphometrics, biomass allocation, oil content, and fatty acid composition is fundamental for identifying promising genotypes and optimizing their use under different environmental and production conditions.

From a conservation perspective, the differentiation observed among sites highlights the importance of preserving germplasm while considering both genetic structure and environmental heterogeneity. The contrasting profiles observed at sites such as Paso Real, characterized by high pulp biomass and pulp oil content, and Turrubares, characterized by high kernel dry mass and kernel oil content, suggest the existence of site-specific phenotypic variation that may be relevant for germplasm management. These patterns are consistent with previous studies reporting geographic clustering, phenotypic differentiation, and genetic structure in *A. aculeata* populations from Costa Rica and Brazil (Alfaro-Solís et al. 2020; de Sá et al. 2022; Díaz et al. 2021; Navarro-Cascante et al. 2023; Morales-Marroquín et al. 2026). However, phenotypic traits should not be interpreted as direct indicators of genetic differentiation unless they are explicitly tested. Rather, they may reflect the combined influence of genetic background, local environmental conditions, and genotype-by-environment interactions.

The Osa Peninsula population deserves particular attention for conservation because it exhibits distinctive fatty acid profiles and has been reported to share genetic affinity with southern populations from Panama (Morales-Marroquín et al. 2026). These findings suggest that the Osa Peninsula may represent a unique genetic and adaptive resource within the Costa Rican germplasm. Considering that Mesoamerican populations show lower genetic diversity than South American gene pools do (Díaz et al. 2021; Navarro-Cascante et al. 2023), conservation strategies should integrate *in situ* preservation of locally adapted germplasm with *ex situ* collections that bring together representative genotypes from all sites. Although the Costa Rican germplasm shows significant variability, its range may be narrower than that reported for broader Neotropical populations, suggesting that the incorporation of genetic material from other regions could increase trait diversity and enhance future breeding progress.

From a breeding perspective, the observed variation supports the development of *A. aculeata* as a multipurpose crop and highlights the importance of integrating multiple traits into selection criteria. Fruit size alone is not sufficient for predicting oil production potential, since oil yield depends on both tissue biomass and oil concentration. This was evident in Paso Real, whose pulp dry mass and pulp oil content were the highest despite not having the largest fruits, whereas Abangares and Turrubares produced larger fruits but did not have the highest pulp oil content. Therefore, selection programs should combine fruit morphometrics, pulp and kernel biomass, oil concentration, and fatty acid composition rather than rely on fruit size as a single selection criterion (Ciconini et al. 2013; da Conceição et al. 2015; Alfaro-Solís et al. 2020; Vargas-Carpintero et al. 2021).

The site-specific patterns observed in this study suggest different breeding targets. Paso Real represents a valuable source of germplasm for mesocarp oil production because of its high pulp biomass and pulp oil content. In contrast, Turrubares is particularly relevant for kernel oil production because of its high kernel dry mass and high kernel oil content. Río Negro may be useful for selecting genotypes with higher lauric acid content in the kernel, whereas Orotina, Nicoya, Cuajiniquil, and Osa Peninsula may contribute to the development of high oleic acid mesocarp oil profiles. Abangares and Río Negro, which exhibited intermediate but relatively balanced values for several fruit and oil traits, may be useful sources for selecting broadly adaptable germplasms. Conversely, although Nicoya and Cuajiniquil showed smaller fruits and lower biomass or oil content for several traits, they should not be excluded from conservation efforts, as they may carry unique alleles or locally adapted traits that could become valuable under specific environmental conditions.

Environmental factors may also contribute to the observed variation; however, environmental variables were not directly evaluated in this study. Therefore, future research should assess genotype-by-environment interactions through multiple location trials. Such approaches would help determine the stability of fruit traits, oil content, and fatty acid composition across production environments. The contrasting patterns of oil accumulation between pulp and kernel further suggest opportunities for crossing genotypes with complementary traits, such as high pulp oil content, high kernel oil content, and desirable fatty acid profiles. These strategies could support the development of cultivars adapted to diverse production systems and industrial applications.

Conclusion

This study increases the current knowledge of *Acrocomia aculeata* in Mesoamerica by incorporating underrepresented populations from Costa Rica and integrating phenotypic, biochemical, and geographic data. The results confirm previously described patterns of the species, including the predominance of oleic acid in mesocarp oil and lauric acid in the kernel, while also revealing site-specific variation, particularly in Cuajiniquil and the Osa Peninsula. These findings provide a valuable reference for the characterization and management of genetic resources in the region. The variation observed in fruit morphometrics and oil-related traits, even within a relatively small geographic area, emphasizes the importance of evaluating germplasm at the local level. Such variation represents a relevant resource for the identification of superior genotypes, the definition of ideotypes, and the conservation of adaptive diversity. Together with emerging genetic and genomic information, these results support the development of breeding strategies that exploit structured variation to improve oil-related traits across environments.

The differentiation between mesocarp oil with a high content of oleic acid and kernel oil rich in lauric acid highlights the multipurpose potential of *A. aculeata* and its relevance for diverse value chains, such as food, health-related products, and industrial applications. Finally, the phenotypic differentiation and diversity observed across all the sites reinforce the need for the establishment of representative germplasm collections and the implementation of site-specific conservation strategies. Together, these results highlight the relevance of integrating phenotypic diversity into conservation and breeding programs to support the domestication and sustainable use of *A. aculeata*.

Declarations

Competing interests:

The authors declare that they have no conflicts of interest and that they have no relevant financial or nonfinancial interests to disclose.

Compliance with Ethical Standards

Ethical statement: The collection of samples in this research was approved by the National Commission for the Management of Biodiversity in Costa Rica under permit number CM-ITCR-004-2021.

Declaration of generative AI and AI-assisted technologies in the editing process

During the preparation of this manuscript, the authors used ChatGPT and Copilot. These AI tools helped to improve clarity and conciseness throughout the writing process, to improve the readability of English, and to polish the language. All AI editing suggestions were carefully reviewed, edited, and approved. The final analysis, conclusions, and interpretations represent our views and expertise.

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Author Contribution

E.A.S, D.A.A and E.A.V obtained the funds; E.A.V, E.A.S, N.Z and D.A.A conceptualized the research; N.Z, E.A.S and D.A.A collected the samples at the sites of study; P.S.C, A.G.F, J.I.G.R, and E.A.V performed the characterization of fruit biometrics and oil content and extracted the oil for fatty acid profiles; C.C and C.V.H performed the GC analysis to obtain fatty acid profiles; and E.A.V and A.G.F performed the statistical analysis. E.A.V and A.G.F developed the first draft, and all the authors read, edited, and approved the final manuscript.

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Data Availability

The data supporting the findings of this study are provided in the main tables and supplementary tables. Additional raw data are available from the corresponding author upon reasonable request.

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