Journal of Tropical Resources and Sustainable Science
Website : http://journal.umk.edu.my/index.php/jtrss/
eISSN : 2462-2389
Vol: 14, Issue 2, 2026, 316-324
DOI: https://doi.org/10.47253/jtrss.v14i2.2044

RESEARCH ARTICLE

Morphological delimitation of *Durio dulcis* Becc. and *Durio graveolens* Becc. based on comparative leaf traits

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ARTICLE HISTORY
Received : 14 January 2026
Accepted : 1 February 2026
Online : 30 June 2026

KEYWORDS
Durio dulcis,
Durio graveolens,
taxonomic delimitation,
diagnostic characters,
cluster analysis,
germplasm characterization

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ABSTRACT

This study presents a comparative analysis of leaf morphology in *Durio dulcis* and *Durio graveolens*. A total of 12 accessions were analysed using 35 leaf morphological parameters, including leaf organisation, structure, and surface characteristics. The leaf specimens were obtained from the MARDI gene bank in Jerangau, Terengganu, and examined using standardised botanical methodologies. Cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) method based on Gower's similarity coefficient demonstrated clear interspecific separation, indicating clear morphological differentiation between the two species. Although both species exhibited similar characteristics, including simple leaf type, petiolate attachment, and entire margins, significant variations were observed in petiole width (broader in D. graveolens), leaf sizes (larger in D. graveolens), apex and base morphology, leaf shape variability, venation clarity, and trichome distribution (denser abaxial indumentum in D. graveolens). Fourteen morphological characteristics were identified as key diagnostic markers for species delimitation, including petiole width (upper and base), leaf length and width, apex angle and shape, and venation clarity. These findings highlight the significance of detailed leaf morphology in *Durio* classification and provide vital baseline data for conservation, phylogenetic analysis, and future crop enhancement research.

1. INTRODUCTION

The genus *Durio* Adans. (Malvaceae) comprises approximately 30 to 31 tropical tree species of notable ecological, cultural, and economic value. In Malaysia, 24 species have been identified, with 13 in Sabah, 16 in Sarawak, and 13 in Peninsular Malaysia (Thorogood et al., 2022). While around one-third of these species produce edible fruits, only *D. zibethinus* has been widely studied from all aspects and commercially cultivated (Aziz & Jalil, 2019). Although the fruit characteristics of *Durio* often attract both public and scientific attention, their leaf morphology remains vital yet underexplored in understanding species delimitation, ecological adaptation, and evolutionary relationships within the genus, especially in edible wild species such as *Durio dulcis* Becc. and *D. graveolens* Becc.

Vegetative identification, especially based on leaf morphological traits, is critical in *Durio* taxonomy because reproductive structures are seasonal and often absent during field surveys. This limitation poses challenges for identifying non-fruiting saplings in nurseries, natural regeneration plots, and forest inventories, where accurate species identification is essential for conservation planning, ecological studies, and germplasm management. Consequently, reliance on vegetative characters, particularly leaves, becomes indispensable for distinguishing closely related *Durio* species under non-reproductive conditions.

Given the limited exploration of vegetative traits in previous studies, leaf morphological characteristics are widely acknowledged as essential tools for infrageneric classification, species characterisation, and the elucidation of phylogenetic relationships (Qiu et al., 2023), particularly among closely related taxa. Previous taxonomic treatments of *Durio* have largely focused on gross vegetative characters such as leaf shape, size, venation, indumentum, and general petiole form, primarily within descriptive or floristic frameworks (Idris, 2011; Lim, 2012a, 2012b). Nevertheless, fine-scale quantitative leaf traits possessing potential diagnostic significance have remained insufficiently investigated. Notably, petiole width and leaf apex angle have not previously been identified or evaluated as diagnostic characters in *Durio*, and their taxonomic utility has not been assessed in any comparative or multivariate context. This represents a critical gap in vegetative-based species delimitation within the genus, particularly for morphologically similar taxa.

Leaf morphological traits in plants not only reflect underlying genetic divergence but also provide insights into environmental interactions and adaptive strategies across diverse habitats (Feijó et al., 2020). Historically, *D. dulcis,* locally known as "durian lai", has been reported to occur in mixed dipterocarp forests on sandy clay soils and friable clay loams, ranging from lowlands to hillsides and ridges, and occasionally on limestone at elevations between 20 and 800 m (Lim, 2012a). In contrast, *D. graveolens*, locally known as "dalit", is found in wet lowland forests with clay-rich soils, including shale ridges, and at elevations up to 1,000 m (Lim, 2012b). Their broad altitudinal distributions provide an opportunity to examine both shared and distinctive leaf traits potentially reflecting shared ancestry or divergent evolutionary pressures.

Recent discoveries of new *Durio* species further underscore the genus's potential as a valuable reservoir of genetic resources (Thorogood et al., 2022). Accordingly, this study investigates and compares the leaf morphological characteristics of 12 accessions across 35 parameters from *D. dulcis* and *D. graveolens*. Rather than merely describing leaf traits, this study aims to re-evaluate commonly used characters and identify newly identified diagnostic traits using comparative and multivariate analyses. The study is guided by the hypothesis that, despite ecological overlap, these two species exhibit a combination of shared and diagnostic leaf morphological traits that enable reliable species delimitation under vegetative conditions. By identifying overlapping features indicative of close phylogenetic relationships and distinctive traits supporting species-level identification, this study highlights the significance of vegetative morphology in *Durio* taxonomy, conservation, and crop improvement. Moreover, detailed morphological characterisation provides essential baseline data for plant breeding and genetic studies, where accurate evaluation of vegetative traits supports effective germplasm selection and breeding strategies (Dash et al., 2019).

2. MATERIALS AND METHODS

2.1. Sample Collection

Leaf samples were collected in December 2024 from the durian gene bank at the Malaysian Agricultural Research and Development Institute (MARDI), Jerangau, Ajil, Hulu Terengganu. Two species from the genus *Durio* were selected for this study, with a total of six accessions per species sampled, resulting in a total of 12 accessions. Each accession represents a distinct individual tree within the MARDI durian gene bank, and all sampled trees were spatially separated within the collection. For each accession, ten (n = 10) fully expanded, mature leaves were collected from a single tree to ensure consistency in developmental stage and to provide sufficient replication for morphological analysis. The accessions of *D. dulcis* were coded as DDJ 001–DDJ 006, while those of *D. graveolens* were coded as DGJ 001–DGJ 006. Only healthy leaves were collected to ensure consistency in morphological analysis. To maintain uniformity in developmental stages, the selected leaves were carefully examined and immediately preserved for further study.

2.2 Herbarium Specimen Preparation

In addition to morphological analysis, collected leaf samples were also processed for herbarium specimen preparation by following standard herbarium protocols, according to Bridson & Forman (1998) with minor adaptations. Leaves were carefully pressed and dried using a plant presser with newspaper and cardboard, ensuring proper arrangement to maintain structural integrity. The specimens were then mounted on herbarium sheets and labelled with detailed collection information, including species name, accession details, collection location, and date.

Voucher specimens were deposited in the Herbarium Room, Department of Plant Science, Kulliyyah of Science, International Islamic University Malaysia (IIUM), Kuantan, Malaysia, for future taxonomic studies and verification. The sampled trees are part of the MARDI durian gene bank. They are identified and maintained by MARDI based on their planting location within the gene bank, as no formal institutional accession numbers are assigned. The study-specific accession codes (DDJ 001–DDJ 006 and DGJ 001–DGJ 006) are linked to these location-based records to ensure traceability of the sampled material.

2.3. Leaf Morphological Analysis

A total of 35 leaf morphological parameters were examined to assess variations between *D. dulcis* and *D. graveolens*. The parameters were divided into three sections (leaf organisation, leaf structure, and leaf surface), which include measurements of leaf length, leaf width, petiole length, leaf shape, apex shape, base shape, venation patterns, margin characteristics, and other relevant traits. Standard botanical measurement techniques were employed to ensure accuracy and consistency in data collection. In this study, quantitative measurements of length were obtained using a ruler, while angles were measured using a protractor. The leaf surface colour was determined using the Royal Horticultural Society (RHS) Colour Chart, ensuring standardised and precise colour identification.

Basic descriptive statistics (*M* ± *SD*) were calculated for key quantitative traits to summarise intra- and interspecific variation and to provide a statistical basis for subsequent characterisation. For multivariate analysis, continuous quantitative traits were converted into discrete character states using categorical thresholds. These thresholds were defined based on observed natural breaks in the data distribution, overlap patterns between species, and commonly used botanical descriptors. This approach reduced the influence of measurement noise, enhanced repeatability, and allowed for the integration of both quantitative and qualitative traits within a single analytical framework.

2.4. Data Analysis

Morphological data were analysed using cluster analysis implemented in the Multivariate Statistical Package (MVSP). Observed morphological traits were first transformed into descriptors and subsequently encoded as character states for multivariate analysis. Descriptive statistics (*M* ± *SD*) for selected quantitative traits were provided to complement the categorical data and to support the interpretation of morphological variation. Similarity among accessions was calculated using Gower's general similarity coefficient, which is appropriate for datasets comprising mixed data types (quantitative and qualitative characters). A phenogram was constructed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA), a widely applied clustering method in phenetic and taxonomic studies. Clustering patterns were interpreted to assess morphological similarity, intraspecific variation, and species-level differentiation. All measurements and analyses followed standard procedures to minimise biases and enhance analytical robustness.

3. RESULT AND DISCUSSION

A total of 35 leaf morphological traits were assessed across twelve accessions representing *Durio* graveolens (Figure 1) and *Durio* dulcis (Figure 2), with six accessions examined per species (Table 1). These traits comprised both quantitative measurements and qualitative characters. To minimise environmental variation, all leaf samples were collected from mature individuals growing under similar site conditions. This approach allowed morphological differences to be attributed primarily to genetic divergence rather than ecological factors such as sunlight exposure or rainfall variation.

Overall, both species exhibited a suite of shared morphological features typical of the genus *Durio*. All accessions possessed simple leaves with symmetrical laminae in an alternate arrangement with entire margins and attached petioles. Additionally, the presence of petioles with swollen bases was consistently observed across both species. These traits reflect a conserved morphological pattern and support the taxonomic placement of the studied accessions within the genus.

Despite these shared features, several morphological traits showed clear interspecific differences. With respect to the petiole, one of the most distinguishable characteristics was the petiole width. *Durio graveolens* accessions exhibited broader petiole widths, with upper widths ranging from 0.30 to 0.33 cm and lower widths from 0.19 to 0.22 cm. In contrast, *D. dulcis* accessions had narrower petioles, with upper widths of 0.22 to 0.25 cm and lower widths of 0.15 to 0.17 cm. While petiole length exhibited some variation, it ranged from 1.39 to 2.56 cm across all accessions, with substantial overlap between the species. As such, petiole length was not found to be a reliable character for species delimitation in this context.

Leaf size also served as a significant differentiating character. *D. graveolens* consistently displayed larger leaves, with lengths ranging from 13.72 to 16.81 cm and widths (measured at the widest point) from 5.22 to 5.59 cm. In comparison, *D. dulcis* leaves were shorter and narrower, with lengths of 10.23 to 12.30 cm and widths of 3.72 to 4.92 cm.

Measurements of leaf apex and base angles further revealed species-level differences. Although both species shared an obtuse base angle (ranging from 121° to 149°), their apex angles were more distinctive. *D. graveolens* exhibited broader apex angles, ranging from 47.5° to 73.5°, whereas *D. dulcis* displayed narrower apex angles, ranging from 22.5° to 31.0°. Apex shape also differed: *D. dulcis* accessions were consistent in having a cuspidate apex (Figure 3C), while *D. graveolens* exhibited greater variability, including truncate (Figure 3A), convex (Figure 3B), or both apex shapes within single accessions.

Variation was also observed in the base shape of the leaf. All *D. graveolens* accessions showed a uniformly convex (Figure 4A) and rounded (Figure 4B) base, while *D. dulcis* accessions exhibited two types: rounded bases (in DDJ 001, DDJ 003, DDJ 004, and DDJ 005) and convex-rounded forms (in DDJ 002 and DDJ 006). In terms of overall leaf shape, *D. graveolens* demonstrated greater diversity, with three distinct forms, which are oblong (Figure 5A), obovate (Figure 5B), and elliptic (Figure 5C), documented among its accessions. Conversely, *D. dulcis* accessions were limited to oblong and elliptic shapes.

Leaf colouration on the adaxial (upper) surface did not show species-specific patterns, with both species exhibiting moderate olive-green and greyish olive-green hues. However, differences emerged in the abaxial (lower) leaf surface. *D. graveolens* accessions exhibited a wider spectrum of colours, including moderate olive brown (DGJ 001), light olive brown (DGJ 002), light greyish olive (DGJ 003, DGJ 004, DGJ 005), and greyish yellow green (DGJ 006). In contrast, *D. dulcis* accessions were more restricted in their lower leaf colouration, exhibiting light greyish olive (DDJ 001), greyish yellow green (DDJ 002, DDJ 004, DDJ 005, DDJ 006), and light yellowish brown (DDJ 003).

Figure 1: Representative leaves of *Durio graveolens* from each accession (left to right: DGJ 1–DGJ 6). (A) Upper surface; (B) Lower surface of leaves

Figure 2: Representative leaves of *Durio dulcis* from each accession (left to right: DDJ 1–DDJ 6). (A) Upper surface; (B) Lower surface of leaves.

Differences were also noted in venation clarity and the density of trichome on the abaxial leaf surface. *D. graveolens* typically displayed semi-obvious venation (Figure 6A) and has a denser abaxial indumentum (tomentose + lepidote), whereas *D. dulcis* accessions had indefinite venation patterns (Figure 6B) with less dense abaxial indumentum. Although relatively subtle, this distinction contributes to overall species diagnosis.

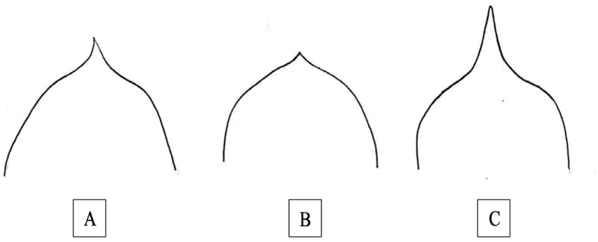

Figure 3: Illustration of leaf apex shape variations observed across *Durio dulcis* and *D. graveolens* in this study. (A) Truncate apex; (B) Convex apex; (C) Cuspidate apex.

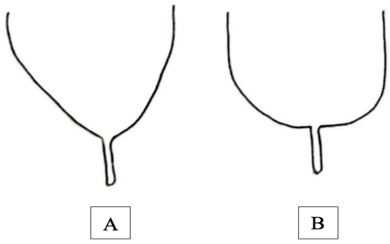

Figure 4: Illustration of leaf base shape variations recorded in the studied *Durio* species. (A) Convex base; (B) Rounded base.

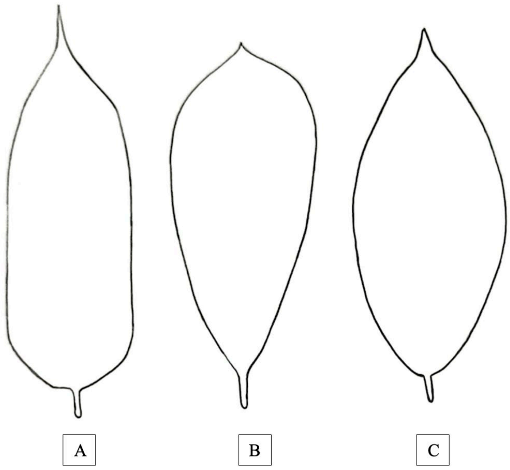

Figure 5: Illustration of leaf shape diversity observed in the studied *Durio* accessions. (A) Oblong; (B) Obovate; (C) Elliptic.

Figure 6: Illustration of leaf shape diversity observed in the studied *Durio* accessions. (A) Oblong; (B) Obovate; (C) Elliptic.

Table 1: Leaf morphological character states for each accession of *Durio dulcis* and *Durio graveolens*. Character presence is indicated by (+), and character absence is represented by grey shading.

No.	Parameter	Characteristics	DDJ 001	DDJ 002	DDJ 003	DDJ 004	DDJ 005	DDJ 006	DGJ 001	DGJ 002	DGJ 003	DGJ 004	DGJ 005	DGJ 006
1	Type	Simple	+	+	+	+	+	+	+	+	+	+	+	+
2	Attachment	Petiolate	+	+	+	+	+	+	+	+	+	+	+	+
3	Arrangement	Alternate	+	+	+	+	+	+	+	+	+	+	+	+
4	Internode length (cm)	< 2.20 cm	+	+	+	+	+	+	+	+	+	+	+	+
5	Petiole features	Upper inflated, base swollen	+	+	+	+	+	+	+	+	+	+	+	+
6	Position of petiolar attachment	Marginal	+	+	+	+	+	+	+	+	+	+	+	+
7	Petiole length (cm)	< 2.60 cm	+	+	+	+	+	+	+	+	+	+	+	+
8	Petiole width (cm) -upper	< 0.26 cm	+	+	+	+	+	+						
		> 0.29 cm							+	+	+	+	+	+
9	Petiole width (cm) -base	< 0.18 cm	+	+	+	+	+	+						
		> 0.18 cm							+	+	+	+	+	+
10	Leaf length (cm)	< 12.40 cm	+	+	+	+	+	+						
		> 13.71 cm							+	+	+	+	+	+
11	Apex length (cm)	< 0.89 cm							+	+	+	+	+	+
		> 0.97 cm	+	+	+	+	+	+						
12	Leaf width (cm) -upper quarter	< 4.02 cm	+	+	+	+	+	+						
		> 4.22 cm							+	+	+	+	+	+
13	Leaf width (cm) -widest part	< 4.93 cm	+	+	+	+	+	+						
		> 5.21 cm							+	+	+	+	+	+
14	Leaf width (cm) -lower quarter	< 4.31 cm	+	+	+	+	+	+						
		> 4.45 cm							+	+	+	+	+	+
15	Symmetry	Symmetrical	+	+	+	+	+	+	+	+	+	+	+	+
16	Apex angle value (°)	< 32°	+	+	+	+	+	+						
		> 46°							+	+	+	+	+	+
17	Apex angle	Acute	+	+	+	+	+	+	+	+	+	+	+	+
18	Apex shape (no. of types)	1 type	+	+	+	+	+	+	+	+	+			+
		2 types										+	+	
19	Apex shape (types)	Cuspidate	+	+	+	+	+	+						
		Convex							+		+			
		Truncate								+				+
		Convex and truncate										+	+	
20	Base angle value (°)	121° - 149°	+	+	+	+	+	+	+	+	+	+	+	+
21	Base angle	Obtuse	+	+	+	+	+	+	+	+	+	+	+	+
22	Base shape (no. of types)	1 type		+				+						
		2 types	+		+	+	+		+	+	+	+	+	+
23	Base shape (types)	rounded		+				+						
		convex and rounded	+		+	+	+		+	+	+	+	+	+
24	Leaf shape (no. of types)	2 types	+	+	+	+	+	+						
		3 types							+	+	+	+	+	+

25	Leaf shape (types)	Elliptic and oblong	+	+	+	+	+	+						
		Elliptic, oblong and obovate							+	+	+	+	+	+
26	Margin type	Entire	+	+	+	+	+	+	+	+	+	+	+	+
27	Lobation	Unlobed	+	+	+	+	+	+	+	+	+	+	+	+
28	Texture	Semi-matte					+	+						
		Matte	+			+			+	+	+	+	+	+
		Shiny		+	+									
29	Colour upper side	Moderate olive green	+	+					+					
		Greyish olive green			+	+	+	+		+	+	+	+	+
30	Colour lower side	Moderate olive brown							+					
		Light olive brown								+				
		Light greyish olive	+								+	+	+	
		Light yellowish brown			+									
		Greyish yellow green		+		+	+	+						+
31	Presence of trichome -upper side	Absent	+	+	+	+	+	+	+	+	+	+	+	+
32	Presence of trichome -lower side	Present	+	+	+	+	+	+	+	+	+	+	+	+
33	Trichome density -upper side	Glabrous	+	+	+	+	+	+	+	+	+	+	+	+
34	Trichome density -lower side	Subglabrous	+	+	+	+	+	+	+	+	+	+	+	+
35	Venation clarity (types)	Semi-obvious							+	+	+	+	+	+
		Indefinite	+	+	+	+	+	+						

To evaluate morphological patterns at the species level, a cluster analysis was performed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on the Gower General Similarity Coefficient, incorporating all 35 measured traits. The resulting phenogram (Figure 7) clearly separated the accessions into two distinct clusters: one comprising all *D. graveolens* accessions (DGJ 001–006), and the other comprising all *D. dulcis* accessions (DDJ 001–006). This result provides strong support for morphological divergence between the two species, despite their sympatric distribution.

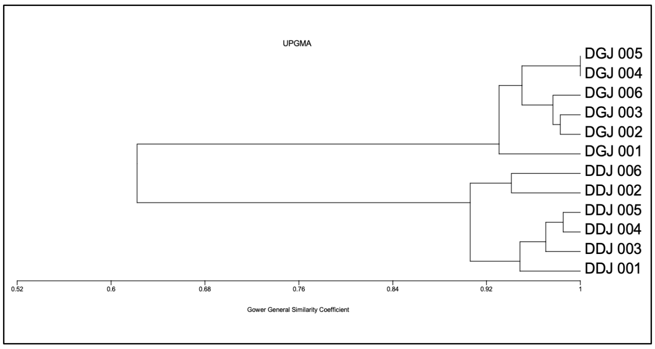

Figure 7: Illustration of leaf shape diversity observed in the studied *Durio* accessions. (A) Oblong; (B) Obovate; (C) Elliptic.

To refine species identification within the genus *Durio*, a subset of 14 morphological traits was identified as the most informative for distinguishing between *D. graveolens* and *D. dulcis* (Table 2). These characters were selected based on their consistent differentiation across all sampled accessions and comprise both quantitative measurements and qualitative descriptors. Their collective diagnostic power highlights the value of targeted vegetative traits for species delimitation, particularly in the absence of reproductive material.

The findings of this study suggest both strong morphological similarities and distinguishing features between *D. dulcis* and *D. graveolens*. The shared traits such as simple leaves, symmetrical lamina, and swollen petiole bases reaffirm their taxonomic placement within the same genus. These characteristics are consistent with previous observations in *D. zibethinus* reported by Idris (2011) and Effendi (2013), which support the morphological conservatism of key features across *Durio* species.

However, distinct differences, particularly in petiole width and leaf size, provide valuable insights into species-level identification. Although petiole length has been employed in other taxonomic studies (e.g. Shamin-Shazwan et al. 2024), its overlap in the present dataset suggests limited diagnostic value in this case. Instead, petiole width emerges as a more promising trait for distinguishing *D. graveolens* from *D. dulcis*, despite being rarely emphasized in prior *Durio* studies.

Table 2: Key diagnostic morphological characters distinguishing *Durio dulcis* and *Durio graveolens*.

No.	Morphological characters	*Durio dulcis*	*Durio graveolens*
1.	Petiole width (cm) – upper	Narrow (< 0.26 cm)	Wider (> 0.29 cm)
2.	Petiole width (cm) – base	Narrow (< 0.18 cm)	Wider (> 0.18 cm)
3.	Leaf length (cm)	Shorter (< 12.40 cm)	Longer (> 13.71 cm)
4.	Apex length (cm)	Longer (< 0.97 cm)	Shorter (> 0.89 cm)
5.	Leaf width (cm) – upper quarter	Narrower (< 4.02 cm)	Wider (> 4.22 cm)
6.	Leaf width (cm) – widest part	Narrower (< 4.93 cm)	Wider (> 5.21 cm)
7.	Leaf width (cm) – lower quarter	Narrower (< 4.31 cm)	Wider (> 4.45 cm)
8.	Apex angle value (°)	≤ 32°	> 46°
9.	Apex shape – number of types	1 type	2 types
10.	Apex shape – type categories	Cuspidate	Convex and truncate
11.	Leaf shape – number of types	2 types	3 types
12.	Leaf shape – type categories	Elliptic and oblong	Elliptic, oblong and obovate
13.	Leaf texture	Matte and semi-matte	Matte
14.	Venation clarity (types)	Semi-obvious	Indefinite

Leaf size likewise showed consistent interspecific divergence and proved informative for species delimitation. Although leaf dimensions have not been widely explored in *Durio* taxonomy, the patterns observed here are comparable to findings in other plant families, where leaf length and width have been successfully applied in species identification (Ardiyani 2015; Liu & Hong 2016). These results suggest that leaf size represents a potentially underutilised yet robust morphological marker in *Durio* systematics, particularly when combined with other diagnostic characters.

Differences in leaf size and petiole thickness may reflect adaptive responses to the contrasting ecological conditions occupied by the two species. *Durio graveolens* is typically associated with wetter lowland forests and clay-rich soils, whereas *D. dulcis* occurs across a broader altitudinal range, including drier or more heterogeneous substrates (Lim 2012a, b). Larger leaves and thicker petioles in *D. graveolens* may therefore be associated with enhanced water transport and mechanical support under moist conditions, while relatively smaller or more uniform leaf traits in *D. dulcis* may represent adaptation to more variable environments. Such ecological associations are consistent with patterns of phenotypic plasticity reported for leaf traits across diverse plant taxa (Tsukaya 2005). However, because all accessions were sampled from a single gene bank environment where macro-environmental conditions were largely uniform, the persistence of these differences suggests that genetic differentiation, rather than environmental variation alone, contributes substantially to the observed morphological divergence. Distinguishing the relative contributions of phenotypic plasticity and genetic control would require common-garden or reciprocal transplant experiments, which were beyond the scope of the present study.

Among the diagnostic characters identified, apex shape, apex angle, and venation clarity demonstrated particularly strong discriminatory value. The consistently cuspidate apex observed in *D. dulcis*, contrasted with the broader and more variable apex forms in *D. graveolens*, supports the taxonomic relevance of apex traits, as similarly reported in Dipterocarpus (Hernández et al. 2020). Although venation clarity and the density of the abaxial indumentum are relatively subtle characters, they provided additional resolution for distinguishing the two species. This finding corroborates previous studies that identified these traits as reliable markers in closely related taxa (Oliveira et al., 2017; Ambarwari et al., 2020) and is consistent with classical descriptions (Beccari, 1889; Lim, 2012a, 2012b). Together, these characters represent some of the most reliable diagnostic features in both field and herbarium contexts.

Lower surface leaf coloration, while often overlooked, provided subtle yet observable variation that could aid in field-based identification. This supports Sundari (2015) and Shan et al. (2019), who emphasized the taxonomic relevance of leaf surface colour in other genera. Venation clarity, although a minor feature, added further resolution to the morphological distinction between the two species. Its taxonomic utility is supported by Oliveira et al. (2017) and Ambarwari et al. (2020), who demonstrated its role in resolving closely related species when other traits showed overlap.

The morphological differentiation observed between *D. dulcis* and *D. graveolens* is also congruent with existing molecular evidence for the genus. A Maximum Likelihood phylogeny by Mursyidin et al. (2023) placed *D. dulcis* and *D. graveolens* within the same major clade, indicating close genetic affinity despite clear species-level separation. This molecular proximity aligns with the substantial overlap in general leaf architecture observed in the present study, while the diagnostic traits identified here provide phenotypic resolution at the species level. Together, these findings demonstrate that fine-scale vegetative characters can effectively complement molecular phylogenetic frameworks by resolving closely related taxa that are genetically similar but morphologically distinct.

Cluster analysis further validated the morphological differentiation between *D. graveolens* and *D. dulcis*, with each species forming discrete and non-overlapping clusters. This pattern is particularly notable given the sympatric occurrence of the two taxa, as it indicates that morphological divergence has been maintained despite potential opportunities for gene flow or environmental convergence. The strong clustering therefore suggests that genetic isolation, potentially reinforced by ecological differentiation, plays a key role in maintaining species boundaries between these taxa. The use of UPGMA in combination with Gower's General Similarity Coefficient proved effective for analysing mixed quantitative and qualitative data and has been widely applied in phenetic and taxonomic studies. The clear separation observed here indicates that the selected morphological characters capture meaningful interspecific variation and are suitable for vegetative-based species delimitation.

Overall, the identification of a focused subset of 14 traits (Table 3) that effectively distinguish the two species underscores the importance of selective trait analysis in plant taxonomy. While several traits overlap and may lead to misidentification if used in isolation, combining multiple diagnostic features enhances reliability in delimitation. When integrated with plastid and nuclear markers, the traits identified here can strengthen future integrative taxonomic approaches by linking phenotypic variation with underlying genetic structure. Such combined frameworks are particularly valuable for *Durio*, where reproductive material is often unavailable and accurate vegetative identification is essential for conservation, germplasm management, and crop improvement.

4. CONCLUSION

This study demonstrates that, despite substantial overlap in general leaf architecture, *Durio dulcis* and *D. graveolens* exhibit consistent and diagnostically informative morphological differentiation. The persistence of these differences across multiple accessions supports their taxonomic distinctiveness and indicates that vegetative traits can provide reliable species-level resolution within *Durio*, even among closely related taxa.

A focused set of leaf characters, particularly leaf size, petiole width, apex morphology, venation clarity, and leaf texture, proved especially effective for distinguishing the two species under non-fruiting conditions. When considered in combination, these traits offer a practical and field-applicable framework for species identification and address a critical limitation in *Durio* taxonomy where reproductive material is often unavailable. The inclusion of visual documentation further strengthens the applicability of these findings by facilitating accurate interpretation of diagnostic features.

More broadly, the results highlight the value of selective morphological trait analysis for resolving species boundaries in morphologically conserved genera. By providing a robust vegetative baseline, this study contributes to the development of more reliable taxonomic tools for conservation, germplasm management, and crop improvement initiatives involving *Durio*. Future work integrating multivariate ordination methods and molecular barcoding data will further refine species delimitation and deepen understanding of the genetic and evolutionary processes underlying morphological variation in this economically and ecologically important genus.

ACKNOWLEDGMENT

This research was funded by the Fundamental Research Grant Scheme (FRGS) (Grant number: FRGS+1+2023+WAB11+UIAM+02+2). We acknowledge and express our gratitude to the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau for their valuable cooperation and support throughout this study.

REFERENCES

Ambarwari, A., Adrian, Q. J., Herdiyeni, Y., Hermadi, I., (2020). Plant species identification based on leaf venation features using SVM. TELKOMNIKA (Telecommunication Computing Electronics and Control)., 18(2), 726–732. https://doi.org/10.12928/TELKOMNIKA.v18i2.14062

Ardiyani, M., (2015). A new species of *Zingiber* (Zingiberaceae) from Enggano Island, Indonesia. Reinwardtia., 14(2), 307–310.

Aziz, A., Mhd Jalil A. M., (2019). Bioactive compounds, nutritional value, and potential health benefits of indigenous durian (*Durio zibethinus* Murr.): A review. Foods., 8(3), 96. https://doi.org/10.3390/foods8030096

Beccari, O., (1889). Durioneae. Malesia., 3(4), 202–260. https://doi.org/10.1002/mmnd.48018890206

Bridson, D. M., & Forman, L. (1998). *The herbarium handbook* (3rd ed.). Royal Botanic Gardens, Kew.

Dash, S. P., Singh, J., Sharma, D., (2019). Morphological characterization of brinjal (*Solanum melongena* L.) germplasm. Journal of Pharmacognosy and Phytochemistry., 8(2), 1574–1578.

Effendi, L. N. (2013). Identifikasi morfologi durian *Durio zibethinus* Sunan dan Brongkol dalam penyusunan basis data keragaman. Master Dissertation, Universitas Sebelas Maret. Indonesia.

Feijó, A., Ge, D., Wen, Z., Xia, L., Yang, Q., (2020). Divergent adaptations in resource-use traits explain how pikas thrive on the roof of the world. Functional Ecology., 34(9), 1826–1838. https://doi.org/10.5061/dryad.sbcc2fr3n

Hernandez, J. O., Maldia, L. S., Pulan, D. E., Buot, I. E., Park, B. B., (2020). Leaf architecture and petiole anatomy of Philippine Dipterocarpus species (Dipterocarpaceae). Bangladesh Journal of Plant Taxonomy., 27(1), 1–14. https://doi.org/10.3329/bjpt.v27i1.47564

Idris, S., (2011). *Durio* of Malaysia, Malaysian Agricultural Research and Development Institute, Malaysia.

Lim, T. K., (2011a). *Durio* dulcis, in: Lim T. K., (ed.), Edible Medicinal and Non-Medicinal Plants: Volume 1. Fruits. Springer., Dordrecht, 550–551.

Lim, T. K., (2011b). *Durio graveolens*, in: Lim T. K., (ed.), Edible Medicinal and Non-Medicinal Plants: Volume 1. Fruits. Springer, Dordrecht, 552–555.

Liu, B., Hong, D., (2016). A taxonomic revision of the *Pourthiaea villosa* complex (Rosaceae). Phytotaxa., 244(3), 201–247. https://doi.org/10.11646/phytotaxa.244.3.1

Mursyidin, D. H., Makruf, M. I., Aliannur, N., (2023). Genetic diversity and relationship of Durian (*Durio* spp.) germplasm based on the internal transcribed spacer (ITS) region: In silico analysis. Planta Tropika., 11(1), 1-10. https://doi.org/10.18196/pt.v11i1.13649

Oliveira, E. F., Bezerra, D. G., Santos, M. L., Rezende, M. H., Paula J. A., (2017). Leaf morphology and venation of *Psidium* species from the Brazilian Savanna. Revista Brasileira de Farmacognosia., 27(4), 407–413. https://doi.org/10.1016/j.bjp.2017.03.005

Qiu, J., Lin, M., Tan, D., (2023). Taxonomic implications of leaf morphology and epidermal anatomy for 14 species of *Gagea* (Liliaceae) from Xinjiang, China. Botanical Studies., 64(1), 33. https://doi.org/10.1186/s40529-023-00405-9

Shamin-Shazwan, K., Shahari, R., Amri, C. N. A. C., Midin, M. R., (2024). Leaf architecture and genome size variation of *Durio zibethinus* L. from Jelebu, Negeri Sembilan, Malaysia. Tropical Life Sciences Research., 35(1), 179. https://doi.org/10.21315/tlsr2024.35.1.10

Shan, Y., Deng, C., Hu, W., Chen, J., Chen, X., Zheng, S., Qin, Q., (2019). First insight into diversity of leaf color of loquat (Eriobotrya) and its potential value in taxonomy. Genetic Resources and Crop Evolution., 66, 143–163. https://doi.org/10.1007/s10722-018-0702-x

Sundari, S., Arumingtyas, E. L., Hakim, L., Azrianingsih, R., (2015). Morphological variation of local durian (*Durio zibethinus* Murr.) on the Ternate Island. In Proceedings of the International Conference on Life Sciences (ICOLIB). University of Jember, Indonesia.

Thorogood, C. J., Ghazalli, M. N., Siti-Munirah, M. Y., Nikong, D., Kusuma, Y. W. C., Sudarmono, S., Witono, J. R., (2022). The king of fruits. Plants, People, Planet., 4(6), 538–547.

Tsukaya, H., (2005). Leaf shape: genetic controls and environmental factors. The International Journal of Developmental Biology., 49(5–6), 547–555. https://doi.org/10.1387/ijdb.041921ht.

