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Distribution and morphological variation of *Stelechocarpus burahol* in Java, Indonesia

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Abstract. *Norantin AA, Djuita NR, Sulistijorini. 2025. Distribution and morphological variation of* Stelechocarpus burahol *in Java, Indonesia. Biodiversitas 26: 4284-4296. Stelechocarpus burahol* is a species historically used in Java as a natural perfume. Understanding its distribution and morphological variation is crucial for conservation given its rarity. This study aimed to provide the first island-wide distribution mapping and the first morphological analysis of *S. burahol* in Java. Field surveys in 16 districts across West, Central, and East Java yielded 54 accessions, collected using exploratory sampling method with geographic coordinates recorded to generate a distribution map. A total of 51 morphological characters from both vegetative and generative organs were observed and analyzed using Unweighted Pair Group Method with Arithmetic Mean (UPGMA) in NTSYS 2.02i, Principal Component Analysis (PCA), and Pearson correlation analysis in RStudio 2023.12.1. Field observations revealed that *S. burahol* remains relatively abundant in Kebumen, Purworejo, Blitar, and Meru Betiri National Park. *S. burahol* exhibits variation in the shape of the canopy, leaves, flower petals, fruits, and seeds. Phenetic analysis grouped accessions into three major clusters: Group I (25 accessions, small subglobose fruits), Group II (27 accessions, medium obovoid fruits), and Group III (2 accessions, large obovoid fruits). These clusters did not correspond to geographic origin, indicating that phenotypic similarity primarily influences morphological variation. PCA confirmed that fruit traits, particularly fruit length, diameter, weight, and flesh weight (eigenvalues > 0.9), were dominant in group separation. Pearson correlation revealed a relationship among key fruit traits. These findings provide baseline data to support future conservation efforts, with priority given to Group III's large-fruited accessions and Group I's forest-associated populations.

Keywords: Annonaceae, biodiversity, conservation, *kepel*, UPGMA clustering

INTRODUCTION

Stelechocarpus burahol (Blume) Hook.f. & Thomson belongs to the family Annonaceae and is distributed across Southeast Asia, including Java Island (Herlina et al. 2018). Blume first described it in 1825 under the name *Uvaria burahol* in Bijdragen tot de Flora van Nederlandsch Indie (Blume 1825). However, Hooker and Thomson (1855) reassigned the species to the genus *Stelechocarpus*, resulting in the current taxonomic designation as *S. burahol*.

Stelechocarpus is a small genus within Annonaceae, with *S. burahol* uniquely cauliflorus (Van Heusden 1995). Morphologically, this species is distinguished by cauliflorous flowers borne on the trunk and ramiflorous flowers on the branches, with imbricate sepals and petals arranged in two whorls, and ellipsoid to obovoid fruits containing several compressed seeds (Backer and Bakhuizen van den Brink 1965). Recent phylogenomic studies have further clarified its placement within tribe Miliuseae, subtribe Winitiinae, together with Sageraea and Winitia (Nge et al. 2024). This species is also marked by relatively large seeds, resulting in a comparatively small amount of fruit flesh (Soeroto et al. 2018). This species has been traditionally consumed in Javanese palaces for its pleasant fragrance after consumption due to anti-halitosis (Amin et al. 2018). It is also used as a raw material for furniture (Karimah et al. 2022) and also exhibits pharmacological potential, including anti-implantation (Suparmi et al. 2015), antibacterial (Indariani et al. 2017), and antioxidant (Herlina et al. 2018). Despite its potential in these fields, *S. burahol* has been reported to be in continuous decline (Umiyah 2005).

While *S. burahol* is not currently listed in the IUCN Red List, this species holds a conservation-dependent status (Mogea et al. 2001), which places it at risk of extinction if conservation efforts are not implemented. Conservation conducted by the Center for Research and Development of Biotechnology and Forest Plant Breeding, Yogyakarta has shown a low survival rate (Fiani and Yuliah 2018). On the other hand, *S. burahol* is further threatened by potential habitat loss driven by the increasing urbanization of Java. Fletcher et al. (2018) stated that habitat loss is the greatest threat to global biodiversity. Sun et al. (2022) showed that the reduction of natural habitats through human land use decreases biodiversity. Likewise, Holden et al. (2024) emphasized that habitat loss is one of the leading causes of global biodiversity decline. Therefore, further conservation efforts are necessary to preserve the existence of *S. burahol*. Studies have also demonstrated the vulnerability of other endemic Annonaceae species, notably *Monanthotaxis bali,* where extensive agricultural encroachment has placed the species at risk of global extinction (Cheek et al. 2023).

One of the fundamental steps in conservation is understanding the level of diversity. The study of morphological diversity is not only helpful in identifying phenotypic variation but also plays an important role in supporting conservation efforts (Cabrera-Toledo et al. 2020; Khadivi et al. 2022; Akhter et al. 2025). Information regarding the location and variation of a species is valuable for documenting floral and habitat diversity and supporting its potential future applications (Djuita et al. 2016). Morphology-based approaches that observe phenotypic characters remain relevant and widely used (Malki et al. 2023; Hariyono et al. 2024). This approach examines phenetic relationships among plants based on shared morphological traits (Hartati et al. 2019). Nevertheless, morphological information alone is not sufficient. Given the limited knowledge of current population locations, mapping the distribution of *S. burahol* is also necessary to identifying existing populations in the field and facilitating conservation actions.

To date, morphological studies on *S. burahol* have been limited to the Yogyakarta region (Handayani et al. 2020; Handayani et al. 2021), leaving a gap in understanding its overall morphological diversity and geographical distribution across Java Island. Given the increasing threat of habitat loss and the limited knowledge of current population locations, this study provides the first comprehensive assessment of *S. burahol* by mapping its distribution, inventorying germplasm, and analyzing morphological variation, which will support conservation strategies for *S. burahol*.

MATERIALS AND METHODS

Study area

Field exploration for this morphological study was conducted between June 2024 to April 2025 across Java Island, Indonesia. Sampling covered 16 locations, including areas in West Java (Bogor and Leuweung Sancang Nature Reserve), Central Java (Banyumas, Kebumen, Wonosobo, Temanggung, Magelang, Purworejo, Klaten, Salatiga, Sragen, and Ulolanang Kecubung Nature Reserve), and East Java (Kediri, Blitar, Malang, and Meru Betiri National Park). These locations were selected based on initial information gathered from literature and local settlements.

Procedures

Distribution mapping and data collection

Having secured all required permits from the relevant authorities (SI.374/K.1/BKW.III/KSA.4.2/B/09/2024: Leuweung Sancang Nature Reserve, SI.149/K.21/TU/KSA. 4.2/B/5/2024: Ulolanang Kecubung Nature Reserve, SI.132/T.15/TU/KSA/8/2024: Meru Betiri National Park), field exploration was conducted using an exploratory sampling method (Rugayah et al. 2004) and morphological observations were conducted based on descriptors of the Annonaceae family, referring to *Annona cherimola* as outlined by Bioversity International (BI 2008). We identified trees as *Stelechocarpus burahol* using the morphological characters described by Van Heusden (Van Heusden 1995). In total, we obtained 54 accessions from 16 study locations, with the following distribution: Bogor (5 samples), Leuweung Sancang Nature Reserve (3 samples), Banyumas (7 samples), Kebumen (7 samples), Wonosobo (1 sample), Temanggung (2 samples), Magelang (2 samples), Purworejo (4 samples), Ulolanang Kecubung Nature Reserve (2 samples), Salatiga (2 samples), Blitar (3 samples), Malang (6 samples), Kediri (3 samples), and Meru Betiri National Park (4 samples).

Each sampling point was georeferenced using a handheld GPS unit (Garmin GPSMAP 60i). We visualized the distribution data using QGIS version 3.43.3. Elevation information was retrieved from the WorldClim global climate database (https://www.worldclim.org/) at a 30 arc-second (~1 km) resolution by Fick and Hijmans (2017), specifically from the elevation layer. The sampling coordinates were imported into QGIS as shapefiles and overlaid with the elevation layer to produce the distribution map.

Accessions were selected based on the presence of mature structures, particularly fruiting organs. In locations where only one tree was found, it was taken as the sample. In locations where more than one tree was present, sampling was directed toward trees showing distinct morphological differences. This approach was applied to capture the widest possible range of morphological variation within each site, rather than randomly selecting accessions. Specimens collected from each accession included leaves, flowers, fruits, and seeds. Plant organs were appropriately cut, labeled with hanging tags for identification, and stored in containers with 70% alcohol to preserve structural integrity for further observation. Traits prone to loss post-harvest such as scent, taste, and texture, were recorded directly during fieldwork. Each accession was photographed to document morphological features. Morphometric measurements employed a digital caliper (± 0.01 mm accuracy) for smaller structures (e.g., sepals and petals), a measuring tape for larger parts (e.g., leaves and fruits), a hagameter to estimate tree height, and a digital scale to record the weight of fruits and seeds. All accessions received labels containing codes and field information, including location, date, elevation, and habitat type.

Morphological character observation

This study directly examined the morphological traits in the field and conducted further observations at the Laboratory of Ecology and Plant Resources, Institut Pertanian Bogor. The analysis measured each trait in multiple replicates per accession: five replicates for leaves and ten replicates for flowers, fruits, and seeds, following the descriptors of *A. cherimola*. Mean values from these measurements were used for subsequent analyses. The study presents the observed accessions of *S. burahol* as descriptive accounts of vegetative and generative organs, group-wise descriptions, identification keys, and supporting morphological photographs. The research examined 51 morphological characters, consisting of 15 vegetative traits, 20 floral traits, and 16 fruit and seed traits. Most characters were adapted from the descriptors of *A. cherimola*, with several modifications reflecting conditions encountered during field exploration. Botanical terminology follows the definitions provided by Hickey and King (2000).

Data analysis

We transformed the measured character data into scored data and treated them as multistate variables. These data were then used to calculate similarity indices through the Similarity for Qualitative Data (SIMQUAL) procedure using the Simple Matching (SM) coefficient. The resulting matrix was applied to perform clustering analysis using UPGMA. The analysis employed NTSYS software version 2.02i, which has been widely applied in morphological variation studies (Rahman et al. 2022; Nurzaman et al. 2024; Vuong et al. 2024; Xu et al. 2024; Yaman et al. 2024). We further extended the analysis using PCA to identify the dominant characters contributing to the clustering patterns (Jalil et al. 2020).

PCA was performed on all 54 scored multistate morphological characters using RStudio version 2023.12.1. Characters with stronger influence on group separation are indicated by longer vector arrows (Jalil et al. 2020). The PCA was to identify dominant morphological characters and to develope diagnostic traits for *S. burahol* accessions. Pearson correlation analysis was conducted using RStudio version 2023.12.1 on the dominant morphological characters identified by PCA to examine relationships among traits, providing practical guidance for breeding or germplasm evaluation.

RESULTS AND DISCUSSION

Distribution of *Stelechocarpus burahol*

During the exploration, *S. burahol* were found in two types: forest areas and residental areas. Fifty-four samples were successfully collected, representing the distribution of *Stelechocarpus burahol* across Java (Figure 1). According to field data, regions where *S. burahol* trees still present include Bogor (Institut Pertanian Bogor; Politeknik Pengembangan Pertanian Bogor; Cipaku Garden), Garut (Leuweung Sancang Nature Reserve), Banyumas (Rawalo Subdistrict; Karanglewas Subdistrict; North Purwokerto Subdistrict; Baturaden Subdistrict), Kebumen (Puring Subdistrict; Gombong Subdistrict; Bulupesantren Subdistrict), Wonosobo (Kaliwiro Subdistrict), Temanggung (Pendopo of Temanggung Regency), Magelang (Rindam IV Diponegoro), Purworejo (Pendopo of Purworejo Regency; Purworejo Subdistrict), Klaten (Pedan Subdistrict), Batang (Ulolanang Kecubung Nature Reserve), Sragen (Tunas Jaya Sejati, Sambungmacan Subdistrict), Salatiga (Pabelan Subdistrict), Kediri (Yayasan Hijau Daun Mandiri; Kandat Subdistrict), Blitar (Mayor of Blitar's Official Residence; Sanankulon Subdistrict), Malang (Bantur Subdistrict; Turen Subdistrict; SMAN 1 Dampit), and Jember (Meru Betiri National Park).

We recorded the presence of this species in various residential areas, including gardens, yards, roadside edges, and government buildings (Figure 2.A, 2.B, 2.C). Residents explained that *S. burahol* was historically not allowed to be planted indiscriminately. The tree was typically placed on either side of the entrance gates to symbolize strength and protection. Such traditions persist today, for example, at the Pendopo of Temanggung District, where *S. burahol* trees stand on both sides of the main building. The historical link to *S. burahol* distribution also emerged in several sampled sites, including Bantur Village, Malang. In this village, the species is regarded as part of the local history. Oral traditions recount that Bantur was once a forested area opened by Kyai Radiman, a follower of Prince Diponegoro. Today, his grave remains in the village, and the continued presence of *S. burahol* is seen as a symbol of social status and historical legacy.

The species remains frequently in Kebumen, Purworejo, Blitar, and Meru Betiri National Park. We also recorded it along the roadside in Kaligesing, Purworejo. In Wonosobo, only a few *S. burahol* trees grew at the Pendopo of Wonosobo District, and none had reached maturity. Security staff explained that the tree had been planted several years earlier but had grown slowly. The highland setting of Wonosobo, characterized by a cold climate, likely contributed to this restricted growth performance based on elevation. We also collected fewer accessions from West Java, where highland areas dominate most of the province. This topography may partly account for the limited distribution in the region.

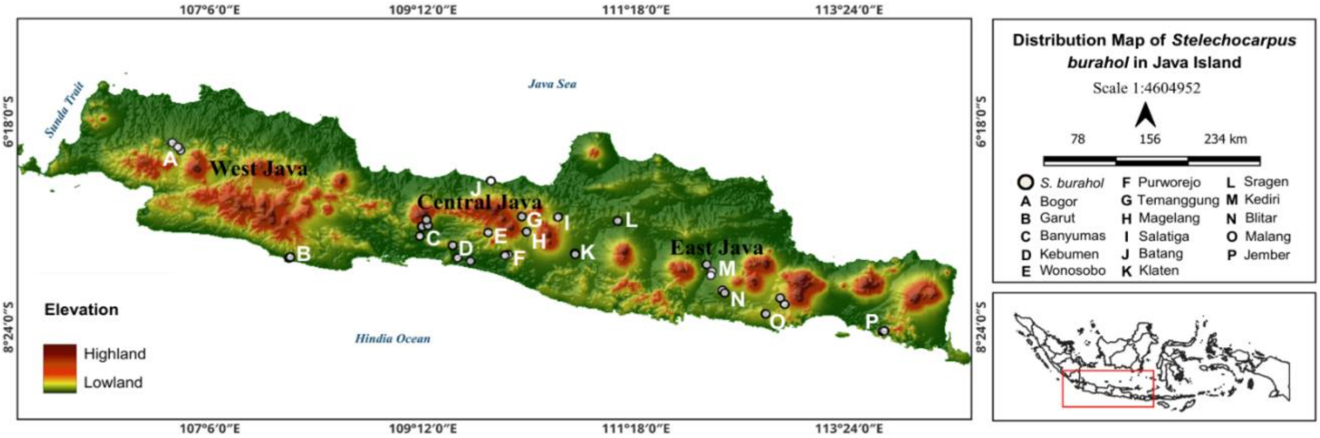


Figure 1. Field-based distribution of *Stelechocarpus burahol* in Java with elevation background

Figure 2. *Stelechocarpus burahol* in residential and forest areas. A-B. *Stelechocarpus burahol* planted in Pendopo of Purworejo Regency. C. *Stelechocarpus burahol* planted in garden (Salatiga), D. *Stelechocarpus burahol* in Leuweung Sancang Nature Reserve, E. natural regeneration of *Stelechocarpus burahol* in Ulolanang Kecubung Nature Reserve. F. *Stelechocarpus burahol* growing along river estuary edges in Leuweung Sancang Nature Reserve

Figure 3. Variation of crown architecture in *Stelechocarpus burahol* across Java Island. A. Pyramidal, B. Columnar

S. burahol also grows in natural forest habitats such as Leuweung Sancang Nature Reserve, Ulolanang Kecubung Nature Reserve, and Meru Betiri National Park, expanding our understanding of its distribution (Figure 2.D). Within these conservation areas, *S. burahol* occurs in primary forests. Lodadi Block and Jambi Payung Block in Meru Betiri National Park are among the zones where mature trees are frequently found. Natural regeneration was observed almost exclusively in these forested areas, as indicated by the presence of seedlings and saplings (Figure 2.E). In Leuweung Sancang, *S. burahol* is typically found along river estuaries and brackish water edges (Figure 2.F), reflecting the reserve's coastal position facing the southern Java Sea.

Morphological variation in *Stelechocarpus burahol*

S. burahol exhibits morphological variation in habit, stem, leaves, flowers, and fruits. The tree can reach heights of up to 19.5 m with an erect growth habit and typically displays two crown architectures: pyramidal and columnar (Figure 3). The shortest recorded (6 m) was found at SMA Negeri 1 Dampit. The tallest (19.5 m) was in Meru Betiri National Park.

The species usually bears a single main trunk with coarse brown bark. Stem diameter can reach up to 59 cm. One distinctive feature of *S. burahol* is the presence of tubercles, which are protruding structures on the stem where flowers and fruits emerge. The number of tubercles varies among accessions, ranging from sparse to very dense. A higher number of tubercles is generally associated with a greater potential for fruit production. Leaves of *S. burahol* are simple, glabrous, and alternately arranged. The adaxial surface is more lustrous than the abaxial surface and exhibits a reddish-pink colouration when young. Leaf blades measure 11.3-22 cm in length and 4.6-7.9 cm in width. Leaf shape varies from elliptic, ovate, to lanceolate; leaf base shape ranges from acute, obtuse, to rounded; and leaf apex shape ranges from acute to acuminate.

S. burahol is a monoecious species exhibiting cauliflorous and ramiflorous inflorescence patterns. Female flowers are yellow, fragrant, and borne directly on tubercles ranging from 8 to 97. Pedicel length varies between 1.97-6.78 cm.

Sepals are free, and petals are arranged in two concentric whorls: outer and inner. Outer petals are ovate or elliptic, while inner petals are elliptic to obovate. Microscopic observations confirmed that the carpels are apocarpous and arranged spirally on the upper floral surface. Each carpel appears numerous. Male flowers are yellowish-green and fragrant, with pedicel length ranging from 0.61 to 2.3 cm. Sepals are free, and petals are arranged in two whorls. Petals are predominantly obovate. Stamens are numerous, compactly arranged into an ovoid structure with a pointed apex.

The fruit peduncle is stout, measuring 3.8-7 cm long and 2-6 mm in diameter. A peduncle can support one to three fruits, although only one typically develops fully. Mature fruits are brown, aromatic, and contain a yellow to pale yellow-orange flesh, measuring 4-7.5 cm in length, 39-59 mm in diameter, and weighing 33-134 g. The mesocarp is soft, sweet, and slightly bitter. Fruit traits varied considerably across accessions, including fruit shape and size, total weight, flesh weight, and seed number per fruit. Two primary forms were identified based on fruit morphology: subglobose and obovoid. The seeds are brown, relatively large, and rounded to elongated. A single fruit may contain up to five seeds, often dominating the fruit volume and leaving limited space for the edible flesh. This reduced flesh is one of the characteristic features of *S. burahol*. Seed variation across Java includes differences in length (2-3 cm), width (1-2 cm), thickness (9-14 mm), and weight (2-5 g). The morphological variations are presented in Figure 4.

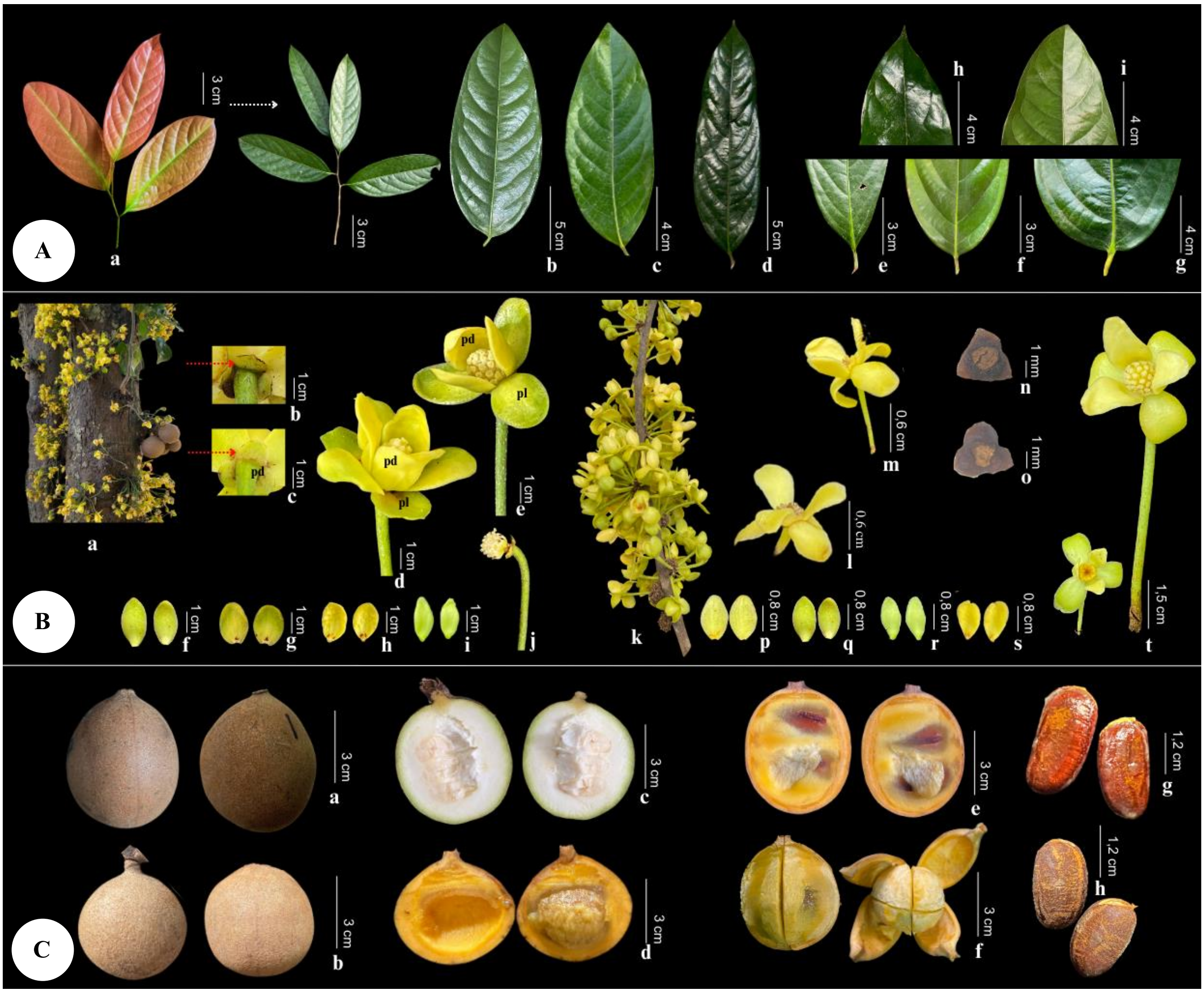


Figure 4. Variation of *Stelechocarpus burahol* in Java. A. Leaves, a. red pinkish leaves, b. ovate, c. elliptic, d. lanceolate, e. acute base, f. obtuse base, g. rounded base, h. acuminate apex, i. acute apex. B. Female and male flower, a. female flowers on tubercles, b. broadly triangular sepal, c. rounded triangular sepal, d. petal number >3, e. petal number: 3, f. outer whorl petal elliptic, g. outer whorl petal ovate, h. inner whorl petal obovate, i. inner whorl petal elliptic, j. pistil, k. male flowers on tubercles, l. short pedicel, m. long pedicel, n. triangular sepal, o. rounded triangular sepal, p. outer whorl petal ovate, q. outer whorl petal elliptic, r. inner whorl petal elliptic, s. inner whorl petal obovate, t. comparison of flower size (male: short, female: long). Pd: inner whorl petal; Pl: outer whorl petal. C. Fruit, a. obovoid fruit, b. subglobose fruit, c. unripe fruit flesh, d. ripe fuit flesh, e. pale orange flesh, f. yellow flesh, g. elongated seed, h. rounded seed

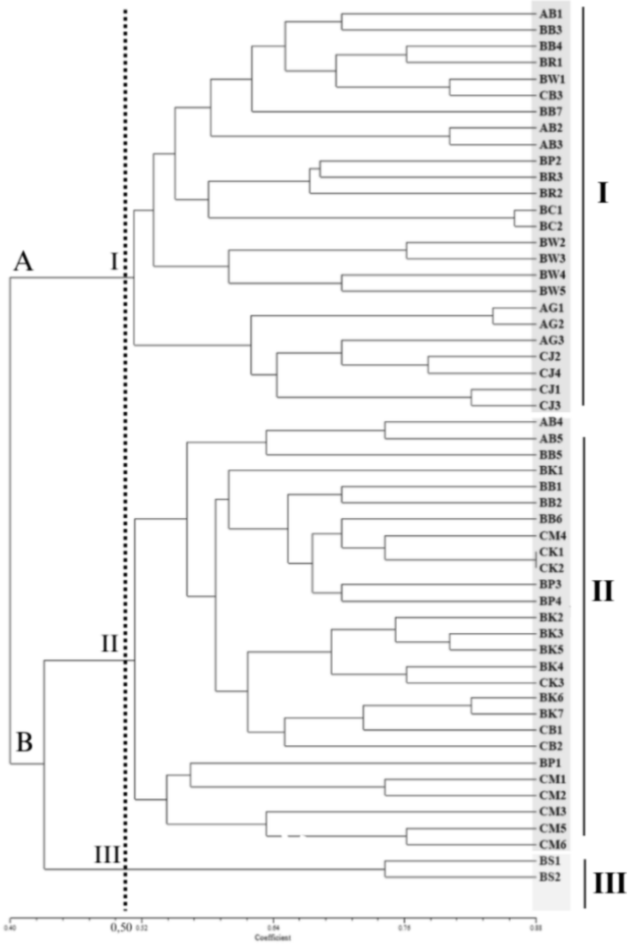


Figure 5. Dendrogram of 54 accessions of *Stelechocarpus burahol* from Java, generated using the UPGMA

Table 1. Cluster-defining fruit characters of the three morphological groups of *Stelechocarpus burahol*

Character	Group 1	Group II	Group III
Prominent midrib	Prominent	Indistinct	Indistinct
Color of female flower	Bright yellow	Pale yellow	Pale yellow
Fruit shape	Subglobose	Obovoid	Obovoid
Fruit length	4.3-5.3 cm	5.4-6.4 cm	6.5-7.5 cm
Fruit diameter	39-45 mm	46-54 mm	53-59 mm
Fruit weight	33-66 g	67-100 g	101-134 g
Flesh weight	13-32 g	33-52 g	53-72 g
Seed shape	Rounded	Elongated	Elongated

Morphological grouping based on phenetic similarity analysis

All accessions of *S. burahol* were grouped at a 40% similarity coefficient. At the 0.43 similarity cutoff, 54 *S. burahol* accessions from Java formed two major groups: Group A and Group B. The morphological character that distinguishes the two is fruit shape: subglobose vs. obovoid. In addition, phenetic analysis also indicated that *S. burahol* clustered into three main groups at a 50% similarity coefficient, designated as Groups I, II, and III (Figure 5). The diagnostic characters of each group, including vegetative and fruit traits, are summarized in Table 1.

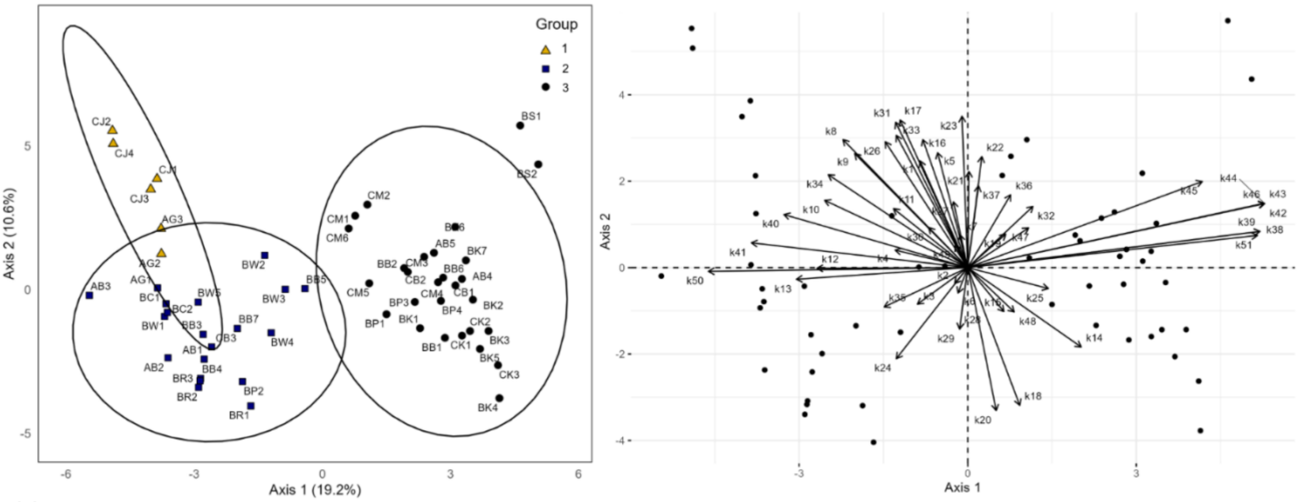
Group I consists of 25 samples, comprising six collections from West Java: Bogor (AB1, AB2, AB3), Leuweung Sancang Nature Reserve (AG1, AG2, AG3); 14 collections from Central Java: Banyumas (BB3, BB4, BB7), Solo Raya (BR1, BR2, BR3), Wonosobo (BW1), Temanggung (BW2, BW3), Magelang (BW4, BW5), Purworejo (BP2), Ulolanang Kecubung Nature Reserve (BC1, BC2); and five accessions from East Java: Blitar (CB3), Meru Betiri National Park (CJ1, CJ2, CJ3, CJ4). Group I is characterized by prominent midribs, bright yellow female flowers, and subglobose fruits that are relatively small with rounded seeds. Group II comprises 27 samples: 2 from West Java: Bogor (AB4, AB5); 14 from Central Java: Banyumas (BB1, BB2, BB5, BB6), Kebumen (BK1, BK2, BK3, BK4, BK5, BK6), Purworejo (BP1, BP3, BP4); and 11 from East Java: Malang (CM1, CM2, CM3, CM4, CM5, CM6), Kediri (CK1, CK2, CK3), Blitar (CB1, CB2). This group shares similar characteristics, such as indistinct midribs, pale yellow female flowers, and medium-sized obovoid fruits with elongated seeds.

Group III comprises only two accessions from Salatiga, Semarang Regency (BS1 and BS2). These accessions had indistinct midribs, bright yellow female flowers, obovoid fruits with obtuse bases, pale orange flesh, and were the largest in size among all samples. Fruit length was 6.5-7.5 cm, diameter 53-59 mm, fruit weight 101-134 g, flesh weight 53-72 g, and the seeds were elongated with five seeds per fruit. The three groups formed did not cluster based on geographic proximity.

Dominant morphological characters and trait relationship

The PCA biplot (Figure 6) illustrates the distribution of accessions along Axis 1 (19.18%) and Axis 2 (10.61%), which together explain 29.79% of the total morphological variation. Longer vector arrows represent characters with more substantial influence on variation. In Principal Component 1, ten morphological characters showed the strongest contributions to variation: fruit length (k42), fruit diameter (k43), fruit weight (k44), flesh weight (k46), fruit shape (k38), fruit base shape (k39), seed shape (k51), seed weight (k50), leaf blade length (k13), and prominent midrib (k12). Principal Component 2 was mainly defined by nine characters, including fresh weight of male flower (k23), sepal shape of male flower (k17), inner whorl shape of female flower (k31), petal length of female flower (k33), male flower pedicel length (k16), leaf blade shape (k8), number of tubercles (k5), leaf base (k9), and petal width of male flower (k22) (Table 2).

The distribution of accessions in PCA space indicated that fruit characters determined separation along PC1. In contrast, floral traits and vegetative traits contributed to PC2. These patterns confirm that fruit, floral, and leaf morphology contribute distinctly to the observed variation. Two accessions (BS1 and BS2) were located outside the 95% confidence ellipse in the PCA biplot, indicating marked differences from the majority of accessions. This result is consistent with the UPGMA analysis, in which BS1 and BS2 also formed a separate group (Group III). Their distinct position is driven primarily by fruit size, as both accessions exhibited the largest fruit dimensions among all samples. Eigenvector loadings (Table 2) further indicate that ten characters in PC1 and nine in PC2 can be regarded as diagnostic traits for distinguishing among *S. burahol* accessions.



A **B**

Figure 6. Results of PCA. A. Biplot showing the distribution of accessions, B. Biplot illustrating morphological character vectors contributing to group differentiation

Identification key of *S. burahol* group:

1 a. Prominent leaf midrib, subglobose fruit, rounded fruit base, yellow flesh, small fruit size (length 4.3-5.3 cm, diameter 39-45 mm, fruit weight 33-66 g), rounded seed …...………………………Group I

b. Less prominent leaf midrib, obovoid fruit, rounded fruit base, pale yellow to orange flesh, medium to large fruit size (length 5.4-7.50 cm, diameter 46–59 mm, fruit weight 67-134 g), elongated seed.……………………………………........…..2

2 a. Pale yellow female flower; inner whorl petals obovate; medium-sized fruit (length 5.4-6.4 cm, diameter 46-54 mm, fruit weight 67-100 g); seed number per fruit: 4……………......................Group II

b. Bright yellow female flower; inner whorl petals elliptic; large-sized fruit (length 6.5-7.5 cm, diameter 53-59.0 mm, fruit weight 101-134 g); seed number per fruit: 5…........….............…Group III

Pearson correlation analysis identified several significant associations among morphological traits (Figure 7). Major fruit traits, including fruit length (k42), fruit diameter (k43), fruit weight (k44), and pulp weight (k46), showed strong positive correlations (r > 0.90). Seed weight (k50) showed negative correlations with these fruit size traits, while the number of seeds per fruit increased with fruit size, ranging from 1-3 seeds in small fruits, 3-4 seeds in medium fruits, and up to 5 seeds in large fruits. Leaf blade length (k13) was positively associated with prominent midrib (k12). In floral traits, petal length of female flower (k33) correlated positively with petal width of male flower (k22). These correlations indicate that both vegetative and reproductive traits contributed to structured patterns of variation in *S. burahol*. We compared fruit morphological traits of *S. burahol* with those of its congener *S. cauliflorus*, and the summary of this comparison is presented in Table 3.

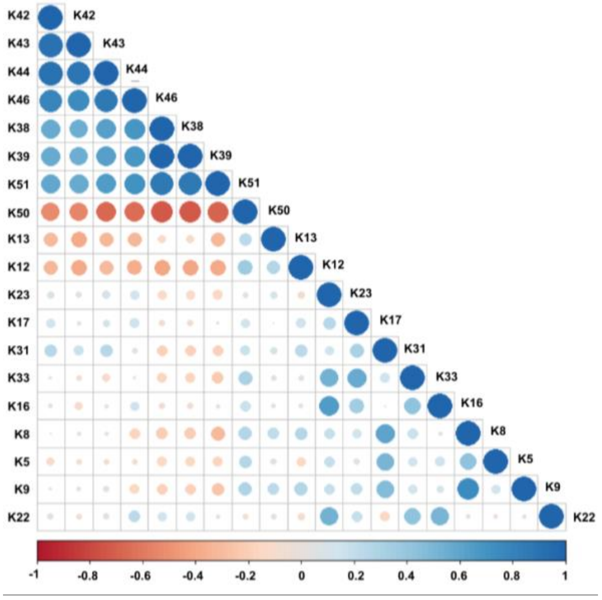


Figure 7. The Pearson correlation matrix of the 19 dominant morphological variables identified through PCA

Table 2. Dominant morphological characters contributing to principal components 1 and 2 based on PCA eigenvectors

Characcter (PC1)	Eigenvalue (PC1)	Character (PC2)	Eigenvalue (PC2)
Fruit length	0.918	Fresh weight of male flower	0.608
Fruit diameter	0.918	Sepal shape of male flower	0.593
Fruit weight	0.918	Inner whorl shape of female flower	0.584
Flesh weight	0.917	Petal length of female flower	0.531
Fruit shape	0.904	Male flower pedicel length	0.515
Fruit base shape	0.904	Leaf blade shape	0.515
Seed shape	0.896	Number of tubercles	0.462
Seed weight	-0.802	Leaf base	0.459
Leaf blade length	-0.530	Petal width of male flower	0.446
Prominent midrib	-0.466	-	-

Table 3. Key fruit morphological traits distinguishing *Stelechocarpus burahol* and *Stelechocarpus cauliflorus*

Character	*Stelechocarpus burahol*	*Stelechocarpus cauliflorus*
Fruit penduncle length	3.9-7.3 cm	2.2-6.5 cm
Number of monocarps	1-3	2-5
Fruit shape	Obovoid to subglobose	Broadly obovoid or ellipsoid to subglobose
Fruit length	4.19-7.5 cm	2.2-7 cm
Fruit diameter	39.2-59 mm	14-45 mm
Fruit color	Brown	Dark brown to black
Number of seeds per fuit	1-5	2-11

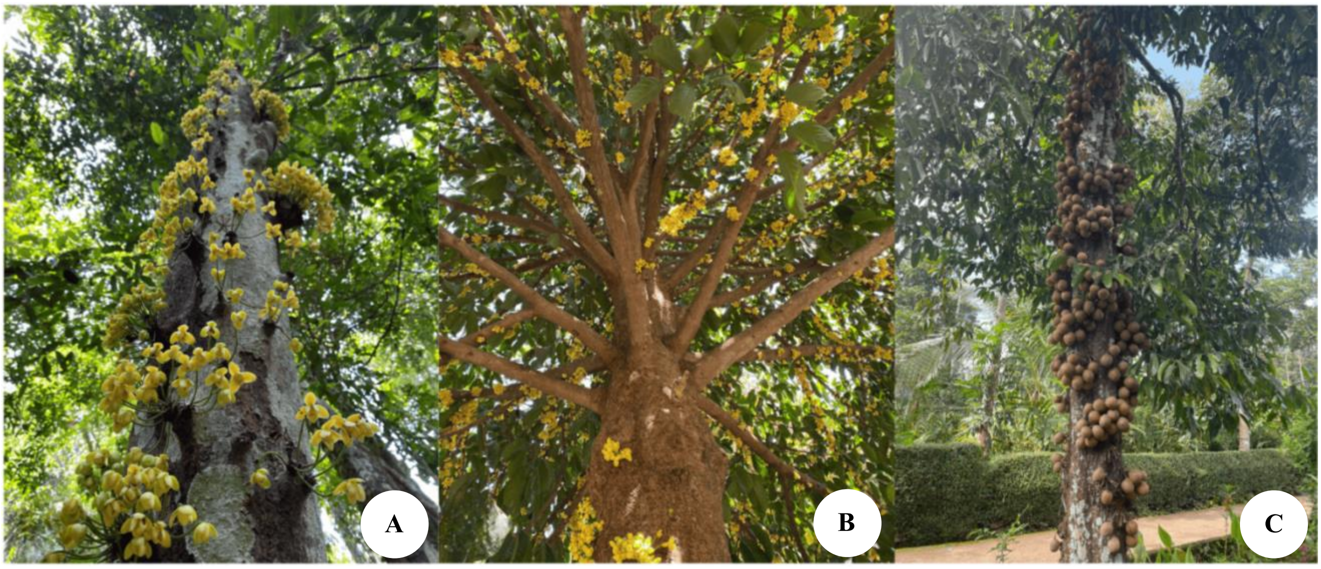


Figure 8. Reproductive morphology of *Stelechocarpus burahol*. A. Female flowers on the main trunk (cauliflorous), B. Male flowers on branches (ramiflorous), and C. Fruits borne in dense clusters on the trunk

Discussion

Interpretation of morphological variation

We provide the first morphological variation analysis of *S. burahol* in Java. *S. burahol* exhibits variation in a wide range of morphological characteristics. In plants, morphological variation is generally influenced by both genetic and environmental factors (Nikmatullah et al. 2023; Richardson et al. 2024). Since this study focused only on morphological traits, molecular and ecological perspectives could not be addressed. Future research should therefore incorporate these approaches for a more comprehensive understanding. Similar to other plant species, *kepel* trees adapt to their growing environments. We found that *S. burahol* accessions in natural forest habitats tend to have greater average tree heights than residential areas.

The high vegetation density in forests restricts light penetration to the understory. Competition within dense forest canopies generally limits light penetration in the understory and drives trees to grow taller to access sunlight (Rozendaal et al. 2020; Matsuo et al. 2024). Conversely, in residential environments such as home gardens, orchards, roadsides, and around government buildings, where canopy cover is less dense, *S. burahol* trees generally grow shorter. Such adaptive responses are also reflected in leaf size. Trees in forest habitats typically have longer leaves than those in residential areas. The occurrence of longer leaves in forest habitats is likely an adaptation to the shaded environment, where broader leaves enhance light capture efficiency, as also reported in *Camellia oleifera* and *Solanum mauritianum* (Zhang et al. 2022; Falla et al. 2023). In contrast, trees in residential areas, which are exposed to higher light intensity throughout the day, tend to develop smaller leaves to reduce transpiration rates. The differences in tree height and leaf length between forest and residential habitats are statistically significant. Forest tree height was significantly higher than in residential areas ($p = 1e\text{-}04$). Likewise, leaf length in forest habitats was significantly greater than in residential areas ($p = 0.0069$).

The leaf variation observed in our study is consistent with previous findings from Yogyakarta, which reported ovate, elliptic, and lanceolate leaf forms (Handayani et al. 2020; Handayani et al. 2021). Unlike leaf size, which appears to be influenced by light availability, leaf shape variation may be driven by other factors. Mutaqin et al. (2024) reported that light intensity, temperature, and water availability play significant roles in shaping leaf morphology. Beyond leaf traits, fruit morphology also provides important characters. Compared to *Stelechocarpus cauliflorus*, another species within the same genus that produces smaller fruits with broadly obovoid to ellipsoid or subglobose forms and turning dark brown to black when dry, *S. burahol* fruits are relatively larger, subglobose to obovoid, and brown when ripe (Van Heusden 1995). A more detailed comparison of fruit traits between *S. burahol* and *S. cauliflorus* is presented in Table 3. Figure 8 shows the reproductive morphology of *S. burahol*. Female flowers were observed both on the main trunk (cauliflorous; Figure 8.A) and on branches (ramiflorous; Figure 8.B), while fruits typically developed in dense clusters along the main trunk (Figure 8.C).

PCA further clarified the contribution of different organs to the observed morphological variation. The first principal component (PC1) was mainly defined by fruit characters, while the second component (PC2) was more influenced by floral and vegetative characters. The ordination also highlighted BS1 and BS2 as distinct accessions, consistent with their separation in UPGMA (Group III), and showed AG and CJ occupying a unique position corresponding to their role as a subgroup within Group I. These findings indicate that fruit morphology is the driver of variation among *S. burahol* accessions, with floral and leaf traits providing additional resolution. However, previous research in Yogyakarta identified leaf shape, leaf size, and bark colour as the primary distinguishing traits among accessions (Handayani et al. 2021). This discrepancy may be explained by differences in plant organs used in the analysis; the previous study focused only on vegetative traits, whereas our study combined leaf, flower, fruit, and seed characters. Although morphological organ size, such as leaves and fruits, can indeed be influenced by environmental conditions (Ningot et al. 2018; Mahla et al. 2022), traditional approaches based on morphological characters remain important and can provide accurate insights into species-specific traits (Saputra et al. 2022).

Interestingly, both studies revealed clustering patterns not based on geographical proximity. The three groups (I, II, III) identified in the UPGMA analysis did not cluster according to their geographical origin. Handayani et al. (2021) reported that environmental and site-specific conditions have little effect on vegetative diversity of *kepel* in Yogyakarta; instead, clustering was more strongly determined by leaf shape, leaf size, and bark color, allowing morphologically similar accessions to originate from different locations. A similar non-geographical clustering pattern has also been reported in *Annona muricata*, where genetic groups identified by SSR markers were not related to geographic origin (Montejo-Mendez et al. 2025). Likewise, Ethiopian barley landraces showed no apparent clustering by geographic origin, with accessions from different regions grouped based on morphological similarity (Gadissa et al. 2021), and similar findings were observed in Korean indigenous buckwheat (Han et al. 2024). In general, the non-geographical clustering pattern may be attributed to environmental influences, gene flow, planting preferences by local communities, or shared genetic factors.

Kepel is historically known as a royal fruit; thus, cultural-historical factors might have contributed to shaping its distribution. For example, *kepel* trees are often found around government buildings, reflecting their symbolic status in the past. While such cultural-historical factors may not directly explain why morphological clustering does not follow geographical patterns, human intervention, for example, the deliberate planting and selection of *kepel*, may also have contributed to this non-geographical clustering. Such practices facilitate human-mediated gene flow, where genetic exchange is driven by human selection and planting. A comparable case was reported in fruit trees of Yaounde, where fewer than 10% of individuals originated from local seeds, and genetic diversity patterns were primarily shaped by human-mediated seed dispersal (Rimlinger et al. 2024). Repeatedly using the same seed sources across regions can lead to genetic uniformity, allowing morphologically similar individuals to occur in different locations. This situation is consistent with findings in urban fruit trees, where planting materials were often obtained from markets or kinship networks rather than local stands, producing genetic diversity patterns unrelated to geographic proximity (Rimlinger et al. 2021). However, interviews with tree owners indicated that most *kepel* trees are inherited plantings with uncertain seed origins. Therefore, it remains unclear whether existing populations derive from a common seed source or from multiple independent introductions.

Environmental conditions are frequently the primary drivers of phenotypic plasticity in plants (Shrivastava and Kumar 2015; Etesami and Maheshwari 2018). In other Annonaceae species, morphological clustering has been shown to vary along environmental gradients. For example, morphological groups in *Annona senegalensis* were shaped by environmental factors (Donhouedé et al. 2023), while

Annona crassiflora exhibited morphological divergence associated with climatic variables, particularly temperature seasonality and precipitation during the warmest quarter (Ribeiro et al. 2016). Field observations in this study also indicated that each morphological group of *S. burahol* resulting from cluster analysis tends to occupy distinct habitat types. Group I, characterized by smaller fruit size, was generally found in forested areas or residential habitats with dense canopy cover. In contrast, Groups II and III, which tend to have larger fruits, were mainly observed in more open habitats with lower canopy cover. Variation in canopy cover directly influences the microclimate below. Higher light intensity in habitats with reduced canopy cover allows photosynthesis to occur more effectively, enabling greater resource allocation to fruit production (Lu et al. 2022; Taneja et al. 2022; Ou et al. 2023). Groups II and III likely benefit from greater light availability, resulting in larger fruit size. However, this interpretation is still based on preliminary field observations, and further quantitative studies are needed to explicitly evaluate the role of environmental factors in driving morphological variation in *S. burahol*.

Implications of morphological analysis results

Similar to *A. cherimola*, which remains underutilized and faces threats to its genetic diversity in its region of origin (Larranaga et al. 2024), *S. burahol* also requires conservation strategies that ensure the safeguarding of its genetic diversity. According to local residents, *S. burahol* fruit is generally consumed for personal use. Some people also occasionally look for *S. burahol* fruit out of curiosity about its taste. However, its commercial potential remains extremely limited. This was observed in Petanahan (Kebumen), where the fruit was found being sold in a local market at a very low price of approximately IDR 3,000 per kg. In other areas, the fruit is often left to rot, reflecting its underutilized economic value. This limited utilization underscores the importance of exploring other perspectives, such as genetic and morphological diversity, in guiding conservation planning. Thus, the morphological clustering analysis provides insights into the conservation of *S. burahol* in Java. However, implementing conservation programs poses challenges (Cornille et al. 2015).

Conservation should not be limited to symbolic planting; it should be based on germplasm resources, considering the existing genetic variation. Genetic diversity is essential as a defense mechanism for species survival. The loss of genetic diversity can reduce the adaptive capacity of populations to future environmental changes and increase their extinction risk (Chen et al. 2025). Genetic diversity, which has evolved over millions of years, provides the foundation for species to withstand climate shifts, pests, diseases, and other environmental stresses. However, it is increasingly threatened by anthropogenic activities such as deforestation, land-use change overexploitation, and climate change (Rimlinger et al. 2021). Therefore, the morphological variation of *kepel* represented by Groups I, II, and III must be preserved through conservation efforts. Effective strategies should focus on maintaining intraspecific morphological diversity. Shaw et al. (2025), highlighted global challenges of genetic erosion and the need for conservation interventions grounded in genetic data. Similarly, Salgotra and Chauhan (2023) emphasized that preserving genetic variation is key for developing cultivars resilient to environmental change. Likewise, Solberg et al. (2024) noted that despite extensive germplasm collections in seed banks, limited taxonomic representation remains a significant threat to the long-term sustainability of biodiversity.

Group I is primarily found in conservation forests such as Leuweung Sancang Nature Reserve, Ulolanang Kecubung Nature Reserve, and Meru Betiri National Park. In these sites, natural regeneration of *kepel* is still observed, indicating that forest ecosystems provide environmental conditions favorable for the species, particularly during the regenerative stage. Umiyah (2005) documented that populations of *S. burahol* in the Meru Betiri buffer zone consisted of mature trees surrounded by naturally regenerating seedlings. Further ecological research in Meru Betiri supports this finding, showing that *kepel* frequently occurs along riverbanks at temperatures of 26-30°C, humidity of 50-85%, Latosol soils with pH 5.5-6.5, and dominant vegetation associations of *Chydenanthus excelsus* and *Sandoricum koetjape*. Natural regeneration is supported by dispersal agents such as flying foxes and rainwater runoff (Heriyanto and Garsetiasih 2005). Factors such as canopy cover, microclimate, soil fertility, and dispersal agents are crucial in maintaining *kepel* populations in natural habitats. In addition to supporting regeneration, conservation forests are relatively free from anthropogenic disturbances, habitat degradation, and land-use change. Counterfactual analysis in Sumatra and Kalimantan demonstrated that villages near protected areas experienced 3.4% lower deforestation rates than control villages beyond a 10 km radius (Morgans et al. 2024). Under these conditions, in situ conservation is the most relevant approach to ensure the sustainability of Group I.

Group III forms a distinct cluster outside the 95% confidence ellipse in PCA and also separates in UPGMA analysis, indicating a marked divergence from other groups. This finding aligns with Khadivi et al. (2022), who reported that individuals outside the confidence ellipse often represent unique traits relative to the main clustering pattern. Among all accessions analyzed, Group III members possess the largest fruit size. Therefore, conserving this group, which consists of only two accessions, is critical, as it may harbor rare alleles associated with agronomic, ecological, or genetic traits. To confirm this, further molecular studies are needed to determine whether the observed morphological differences reflect genetic variation or are solely due to environmental influences. Such molecular studies are relevant given the increasing role of molecular markers in plant genetic analysis (Akhter et al. 2025). Genomic resources can complement these studies; while plastome data in Annonaceae are still scarce, *S. burahol* has already been sequenced (158,837 bp) (Ping et al. 2024).

Field surveys revealed that *S. burahol* trees in residential areas are generally old inherited from previous generations. Most communities perceive the species as having little economic value, resulting in a lack of new planting. In several sites, ripe fruits are left to fall and rot on the ground without being utilized. This situation is exacerbated by the absence of natural regeneration, which poses a risk of morphological variation loss in residential populations. If this trend continues, the possibility of a genetic bottleneck cannot be ignored. Although these trees still contribute to maintaining morphological diversity, particularly in Groups II and III, their long-term survival is not guaranteed. Threats may arise from senescence, logging, lack of community involvement, absence of natural regeneration, and anthropogenic pressures such as land expansion. This condition underscores the importance of conserving Groups II and III by integrating both in situ and ex situ approaches. As Rahman et al. (2021) emphasized, in situ and ex situ conservation must complement one another to capture the full spectrum of plant genetic diversity effectively. In most members of the Annonaceae family, seeds are orthodox, allowing them to be dried and stored in seed banks for the long term (Handayani 2018). Similarly, studies on other Annonaceae, such as *Anaxagorea luzonensis*, have reported orthodox storage behaviour (Lestari and Faya 2024), suggesting that seed-based ex situ conservation may also apply to *S. burahol*. This trait makes seed-based ex situ storage a viable conservation strategy.

Beyond conservation, maintaining the genetic diversity of germplasm resources is essential for ensuring sustainable cultivation (Wang et al. 2025). The observed morphological traits also provide valuable implications for plant breeding. Morphological characteristics are commonly used to determine fruit quality and market preferences (Ullah et al. 2025). Pearson correlation analysis revealed strong positive relationships among major fruit traits (Figure 7). Fruit length (k42) was correlated with fruit diameter (k43; r = 0.918) and fruit weight (k44; r = 0.904). These associations indicate that these traits form a unified axis of fruit size variation. From a breeding perspective, this provides a practical advantage: early-stage selection programs targeting higher edible yield can use fruit length to proxy for flesh weight, reducing the need to measure multiple traits directly. A similar approach was proposed by Okello et al. (2018), who identified fruit length as a practical selection index for both fruit and seed weight in *Tamarindus indica*.

These findings are directly relevant to conservation policy. By highlighting the morphological diversity of *S. burahol*, the study provides a scientific basis for prioritizing in situ protection of Group I within nature reserves, while emphasizing the urgent need to safeguard Groups II and III through ex situ collections and community-based planting schemes. Integrating *S. burahol* into these policy frameworks would preserve its genetic diversity by maintaining native biodiversity and sustaining the species' historical and cultural values in Javanese society.

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