

Leaf Functional Traits Diversity of Mango Wild Relatives (*Mangifera* spp.)

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Abstract. There are 69 species of *Mangifera* distributed worldwide, and approximately 35-40 of these species are found in tropical Asia. This widespread distribution naturally affects the functional characteristics of *Mangifera* species. This research aims to determine the variation in leaf functional traits of *Mangifera* species based on their subgenus (*Mangifera* and *Limus*) and the differences in elevation locations (Bogor Botanical Garden/lowland and Cibodas Botanical Garden/highland). The leaf's functional traits were measured through ten parameters: Fresh Weight (FW), Dry Weight (DW), Leaf Area (LA), Specific Leaf Weight (SLW), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Chlorophyll Content (CC), Stomata Density (SD), Stomata Length (SL), and Stomata Width (SW). The observational data were analyzed using Pearson Correlation, One-Way ANOVA, and Post Hoc Test with Duncan's Multiple Range Test (DMRT). The results show differences in *Mangifera* species' leaf functional traits between subgenus and locations. It was observed that DW, LA, SLA, and CC were higher in the subgenus *Mangifera* than in the subgenus *Limus*. The results also show that the SLW, SLA, LDMC, and CC values are influenced by altitude. The differences in the functional traits of *Mangifera* species are driven by environmental factors that induce phenotypic changes through plasticity, reflecting their adaptation to different environments.

Keywords: altitude, functional characters, leaves, phenotypic plasticity

Citation

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INTRODUCTION

The family *Anacardiaceae* consists of 81 genera, one of which is the *Mangifera* (POWO, 2024). There are 69 species of *Mangifera* distributed worldwide (Sankaran et al., 2021). Approximately 35 to 40 species of mangoes spread across tropical Asia (Fauzia et al., 2021). Mango and its wild relatives (*Mangifera* spp.) are perennial fruit trees widely distributed in Southeast Asia (Melandani et al., 2017). *Mangifera* is mainly distributed in Tropical Asia, with maximum species diversity in the Malay Peninsula, Sumatra, Java, and Borneo (Western Malaysia) (Kostermans & Bompard, 1993; Polosakan, 2016; Sankaran et al., 2021). The primary centre of origin of the genus *Mangifera* is Borneo, whereas Myanmar (Burma)-Siam-Indochina, the Philippines, and the Celebes-Banda-Timor group are considered to be the secondary center of origin of this genus (Kostermans and Bompard, 1993). Eastern India, Assam to Burma, or the Malayan region, is believed to be the origin of the cultivated mango (*Mangifera indica* L.) (Sankaran et al., 2021). Mangoes were first domesticated in India over 4,000 years ago (Mehta, 2017). The domestication of mango (*Mangifera indica*) began in the Indo-Burma region, which includes Northeastern India, Myanmar, and Bangladesh. Mangoes spread to other parts of Tropical Asia through ancient trade and cultural interactions, while their spread to East Africa and Southeast Asia occurred via maritime routes (Mukherjee, 1972).

The widespread distribution of *Mangifera* across various parts of the world naturally affects the functional or phenotypic characteristics of the mango plants, reflecting their adaptation to different growing environments. The distribution of *Mangifera* species is heavily influenced by natural factors affecting their growth, with three main limiting factors:

soil, climate, and altitude. *Mangifera* generally thrives in lowland areas at 0-500 meters above sea level (masl) and 500-1000 masl. However, some *Mangifera* species can survive at altitudes of 1500-2000 masl, and others can live in the lower mountain to highland areas (Kostermans & Bompard, 1993; Polosakan, 2016). Based on their habitats, most *Mangifera* species are distributed in tropical lowland forest regions. However, some species can adapt to extreme conditions, such as nutrient-poor soils or waterlogged areas (Kostermans & Bompard, 1993; Polosakan, 2016).

Mangoes are widely cultivated in Indonesia, exhibiting a diversity of shapes, sizes, flavors, and leaf shapes. As a result, many types of mangoes have been produced. Many of its wild relative species are also found in Indonesia. This diversity is attributed to cross-breeding, natural selection, human influence, and environmental factors. Environmental factors cause variations in each tree's growth of leaves, stems, roots, and fruits (Amalia et al., 2022). One of the conservation sites for mango and its wild relatives is the Botanical Garden. Botanical Gardens serve as ex-situ conservation sites for plants. According to Presidential Regulation No. 93 (2011), a botanical garden is an ex-situ plant conservation area with documented plant collections organized according to themes, bioregions, taxonomic classification patterns, or combinations. Bogor Botanical Garden (BBG) and Cibodas Botanical Garden (CBG) are two such gardens managed by the National Research and Innovation Agency (BRIN) with substantial *Mangifera* collections. These two botanical gardens are located at different altitudes, with BBG classified as a lowland area and CBG as a highland area. This difference in altitude naturally affects the characteristics of the *Mangifera* species collected.

Mangifera species are divided into

two subgenera, *Limus* and *Mangifera*, based on their morphological characteristics, with several sections (Kostermans & Bompard, 1993; Sankaran et al., 2021). Morphological characteristics, particularly of leaves, are typically used to distinguish *Mangifera* species. However, the functional traits of *Mangifera* species leaves have not been extensively studied. These traits are necessary to understand the relationship between species and their habitat conditions. Functional traits are characteristics (morphological, physiological, biochemical, structural, phenological, or behavioral) that represent ecological strategies and determine how plants respond to environmental factors and influence ecosystem properties (Perez-Harguindeguy et al., 2013; Nock et al., 2016). Functional traits include various aspects of the interaction between plants and their environment. These traits encompass how organisms adapt physiologically to the environmental conditions in which they live, such as temperature, humidity, light, nutrient availability, and water stress (Nock et al., 2016). These traits help explain how plants survive, grow, and reproduce in different environments. Among the plant organs that can be observed for their functional traits are leaves. Therefore, analyzing the function-

al traits of *Mangifera* species leaves is necessary to understand their adaptability in diverse habitats. This research aims to compare interspecific leaf functional traits under different subgenus of *Mangifera* (*Mangifera* and *Limus*) and between two different altitudes.

MATERIALS AND METHODS

Research Location

The observation and data collection were conducted at the Bogor Botanical Garden (BBG) and the Cibodas Botanical Garden (CBG) (Figure 1). BBG is located in Jl. Ir. H. Djuanda No. 13, Paledang, Central Bogor District, Bogor City, West Java 1612 (Triastinurmiatiningsih et al., 2021). BBG is 215–260 meters above sea level (masl) (Sudiar et al., 2019). It is one of the oldest botanical gardens in Southeast Asia, covering an area of 87 hectares and housing approximately 15,000 species of trees and plants (Rachmadiyanto et al., 2020). Meanwhile, CBG is located in Cimacan Village, Cipanas District, Cianjur Regency, West Java on the northern slopes of Mount Gede Pangrango, at 1,250–1,425 masl. The total area of the Cibodas Botanical Garden spans 84.99 hectares (Yulianti et al., 2020).

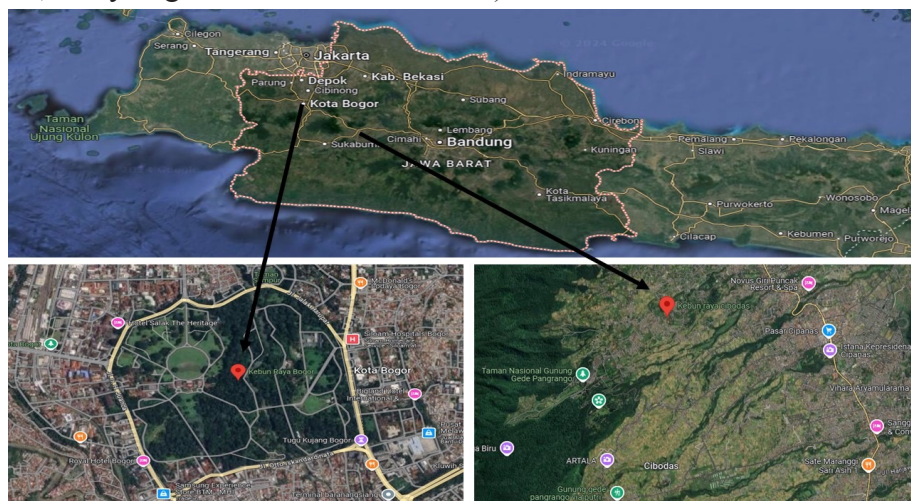


Figure 1. Research Locations: (a) Map of West Java Province, (b) Bogor Botanical Garden, (c) Cibodas Botanical Garden

Data Collection and Analysis

There are 19 species of *Mangifera* in the BBG, while the CBG contains 4 *Mangifera* species. All *Mangifera* species are classified into the subgenus *Mangifera* and *Limus*. The subgenus *Mangifera* consists of *Mangifera gedebe* Miq. VI. D. 5 (BBG), *Mangifera griffithii* Hook. VII. E. 170 (BBG), *Mangifera merrillii* Mukherji. VI. D. 27 (BBG), *Mangifera indica* L. XXIV. A. 48 (BBG), *Mangifera altissima* Blanco. XIX. F. 2 (BBG), *Mangifera similis* Blume. VII. E. 211 (BBG), *Mangifera similis* Blume. IX. C. (CBG), *Mangifera torquenda* Kosterm. VII. E. 210 (BBG), *Mangifera applanata* Kosterm. VI. B. 108a (BBG), *Mangifera casturi* Kosterm. XXIV. B. 57 (BBG), *Mangifera oblingifolia* Hook. F. VI. B. 151 (BBG), *Mangifera rufocostata* Kosterm. VII. E. 178 (BBG), *Mangifera pedicellata* Kosterm. XXIV. A. 156 (BBG), *Mangifera minor* Blume. VII. E. 213 (BBG),

Mangifera laurina Blume. VII. E. 203 (BBG), and *Mangifera laurina* Blume. IX. A (CBG). While in the subgenus *Limus* consists of *Mangifera foetida* Lour. VII. E. 168 (BBG), *Mangifera foetida* Lour. VII. E. 206 (BBG), *Mangifera foetida* Lour. XX. C. 70 (BBG), *Mangifera pajang* Kosterm. VII. E. 222 (BBG), *Mangifera ceasia* Jack ex Wall. VII. E. 209 (BBG), *Mangifera macrocarpa* Blume. VI. B. 8a (BBG), *Mangifera odorata* Griff. XX. C. 68 (BBG), *Mangifera odorata* Giff. XVII A. 7 (CBG), *Mangifera odorata* Giff. IX. B (CBG), *Mangifera foetida* Lour. IX. C. 73 (CBG). Their leaves were collected using a pole pruner with 2–5 meters height. For taller trees, leaves were obtained by climbing the trees. A total of 10 leaves per sample were collected for scanning and measurement of leaf area using ImageJ software, 1 leaf for stomata observation, and 5 leaves for chlorophyll content analysis.

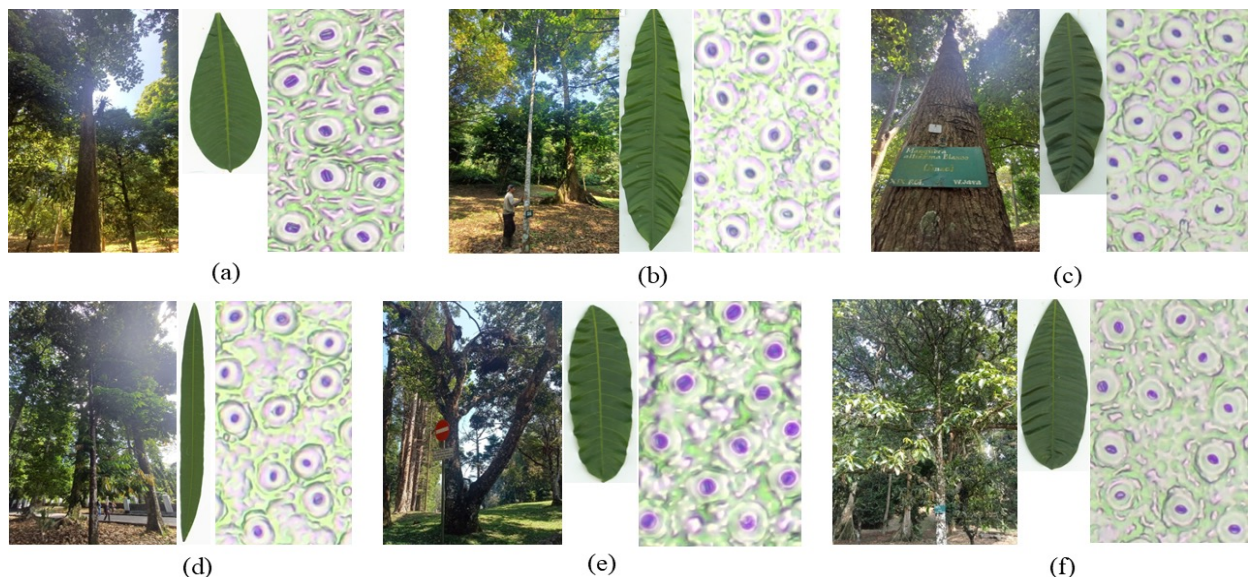


Figure 2. Tree, leaf, and stomata of *Mangifera* (a) *Mangifera applanata* Kosterm., (b) *Mangifera oblingifolia* Hook., (c) *Mangifera altissima* Blanco., (d), *Mangifera macrocarpa* Blume., (e) *Mangifera odorata* Giff., (f) *Mangifera foetida* Lour.

The leaf samples collected are healthy mature leaves without petioles. Ten functional traits were measured based on Perez-Harguindeguy (2013), including: (a) Leaf Area (LA) (cm²): the leaf surface was scanned using a Plustek OpticPro A320 scanner, then analyzed using ImageJ software, (b) Fresh Weight (FW), (c) Dry Weight (DW), (d) Specific Leaf Area (SLA) (cm²/g): the ratio of leaf area to dry leaf weight, in which the fresh weight of the leaves was measured in the field, then put into labeled paper bags and oven-dried at 40°C for 72 hours, (e) Leaf Dry Matter Content (LDMC) (mg/g): the ratio of dry leaf weight to fresh leaf weight, (f) Specific Leaf Weight (SLW) (g/cm²): the ratio of dry leaf weight to leaf area, (g) Chlorophyll Content (CC) (cci): each replicate consisted of 5 fresh leaf samples that were measured for CC using a CCM-200 Plus Chlorophyll Content Meter: at the base, middle, and tip, (h) Stomata Density (SD) and (i) Stomata Size: Stomatal measurements were conducted by coating: the abaxial surface, near the midrib, with transparent nail polish and allowed to dry for about 5 minutes. Afterwards, the nail polish imprint was peeled off using clear tape and placed on a microscope slide. The stomata imprint was then observed under a light microscope (Olympus CX43) at magnifications of 100× and 400×. Parameters such as stomata density (SD), length (SL), and width (SW) were measured using Image Raster 3.0 software. Some examples of *Mangifera* in the BBG and CBG (Figure 2). Statistical tests on the observation data were conducted using Pearson Correlation, One-Way ANOVA, and a Post Hoc Test with Duncan's Multiple Range Test (DMRT).

RESULTS AND DISCUSSION

The correlation between parameters of functional leaf traits

The correlation analysis findings indicate that not all the parameters demonstrate strong correlations (Figure 3). FW, DW, and LA exhibit strong relationships, with FW and DW being significantly correlated with SLW. However, FW and DW do not correlate with LDMC, CC, and SD. FW negatively correlates with SLA and does not correlate negatively with SL and SW, while DW negatively correlates with SL and SW. LA and LDMC do not correlate with SD. LA negatively correlates with SLA, LDMC, SL, and SW. SLW has a significant correlation with LDMC and a low correlation with CC. SLW and CC negatively correlate with SD but do not correlate with SL and SW. LDMC does not correlate with CC. LDMC and SD negatively correlate with SL and SW. CC correlates with SL but has a low correlation with SW, while SL has a strong relationship with SW.

According to the analysis results, about three parameters in particular stand out in the measurement of *Mangifera*'s functional traits, namely: SLW, SLA, and LDMC. In the subgenus *Mangifera*, *M. similis* Blume in CBG has the highest SLA, *M. similis* Blume in BBG has the highest LDMC, and *M. altissima* Blanco in BBG has the highest SLW. In the subgenus *Limus*, *M. macrocarpa* Blume in BBG has the highest SLA, *M. foetida* Lour in CBG has the highest LDMC and *M. foetida* Lour. W. S in BBG has the highest SLW. According to Chown et al. (2004), ecologists have shown that SLA varies depending on environmental factors. Liu et al. (2017) explain that climatic factors have a more

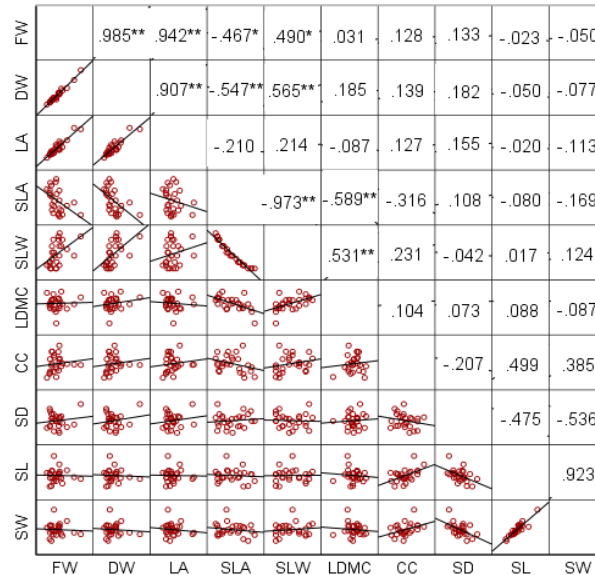


Figure 3. Correlation of variables among *Mangifera* species

Note: * significant $p < 0.05$; ** significant $p < 0.01$; FW= Fresh weight (g); DW= Dry weight (g); LA= Leaf Area (cm²); SLA= Specific Leaf Area (cm²/g); SLW= Specific Leaf Weight (g/cm²); LDMC= Leaf Dry Matter Content (mg/g); CC= Chlorophyll content (cci); SD= Stomata Density; SL= Stomata Length; SW= Stomata Width

significant influence on determining SLA. This is supported by Gong et al. (2011), that plants growing in water-rich and/or nutrient-rich environments have higher SLA because they can obtain sufficient water and/or nutrients for rapid growth, resulting in thinner and larger leaves to enhance light capture and improve their competitive capacity. A high SLW according to Coley (1983), indicates that the leaves are heavier and denser, which is related to resistance against herbivores and extreme environmental conditions, such as drought or high temperatures. Plants with high SLW may have better defense strategies but are less efficient in photosynthesis. According to Wright & Westoby (2002), species with higher dry matter content tend to have larger leaf areas. Plants with high LDMC can withstand environmental disturbances, such as climate change and human activities, resulting in longer life cycles (Hou et al., 2022).

In response to biotic and abiotic stimuli, plants' developmental, physiological,

morphological, behavioral, and life history characteristics can alter. Mostly, evolution and plasticity can lead to phenotypic alterations. Environmental forces impact evolution and plasticity, despite the differences in their phenotypic ranges, recovery rates, and operational timelines (Yamamichi et al., 2011). Key drivers affecting phenotypic traits include CO₂, nutrients, light, temperature, and pests. According to Modolo et al. (2021) light availability changes the trait-trait and trait-growth relationships, consequently integrating phenotypes. For example, in high-light environments, physiological traits related to photosynthetic nutrient use efficiency are strongly associated with growth (Guimarães et al., 2018), whereas in low-light environments, morphological traits related to light interception are strongly associated with growth (Liu et al., 2016). Zhang et al. (2024) stated that leaf nutrient content (nitrogen, phosphorus) and their stoichiometric ratio (N/P) as key functional traits can reflect plant survival strategies and predict ecosystem

productivity responses to environmental changes. Meanwhile, according to Duan et al. (2022) overall, climate is the main driving factor for variation in leaf functional traits. A single genotype can give rise to different phenotypes in response to environmental changes (Yamamichi et al., 2011). Phenotypic plasticity is the capacity of an organism to modify its phenotype in response to changes in its environment (Jebali et al., 2022).

Comparison of functional leaf traits between the subgenus *Mangifera* and *Limus*

Kostermans & Boompard (1993) divided the subgenus *Mangifera* and *Limus* based on the morphological characteristics of their flowers, including inflorescence structure, petal shape and size, the number of fertile stamens, inflorescence type, and the shape of the floral disc. The subgenus *Mangifera* features a floral disc wider than the ovary's base, resembling a cushion, with the filament bases remaining unfused. In contrast, the subgenus *Limus* has a floral disc that is narrower than the base of the ovary, resembling a stalk or sometimes being absent, with the filament bases often fused into an annulus (Kostermans & Boompard, 1993). The subgenus *Mangifera* generally has larger oval or elliptical leaves, with a smooth and glossy surface. In contrast, the subgenus *Limus* has smaller leaves with a simpler shape and a surface that may be rougher. These differences reflect the adaptation and specialization of each subgenus to its respective environment.

Different parameters exist between the subgenus *Mangifera* and *Limus* (Figure 4). The result observed that DW, LA, SLA, and CC were higher in the subgenus *Mangifera*. In contrast, FW, LDMC, SLW, SD, SL, and SW were higher in the subgenus *Limus*.

Leaf Functional traits of the subgenus *Mangifera* and *Limus*

The subgenus *Mangifera* has diverse leaf functional traits (Table 1) *M. oblongifolia* Hook. has the heaviest FW, while *M. gedebe* Miq. has the lowest. The range value of leaf FW for subgenus *Mangifera* species is 1.25-7.64 g. *M. oblongifolia* Hook. has the heaviest DW, while *M. gedebe* Miq. has the lowest. The range value of leaf DW for subgenus *Mangifera* species is 0.57-2.38 g. *M. oblongifolia* Hook. has the largest LA, while *M. minor* Blume. has the smallest. The range value of leaf LA for subgenus *Mangifera* species is 55.132-274.334 cm². *M. similis* Blume. in CBG has the highest SLA, while *M. altissima* Blanco. has the lowest. The range value of leaf SLA for subgenus *Mangifera* species is 50.005-118.536. *M. similis* Blume. in BBG has the highest LDMC, while *M. similis* Blume. in CBG has the lowest. The range value of leaf LDMC for subgenus *Mangifera* species is 0.33-0.57. *M. altissima* Blanco. has the highest SLW, while *M. similis* Blume. in CBG has the lowest. The range value of leaf SLW for subgenus *Mangifera* species is 0.008 - 0.2. *M. pedicellata* Kosterm. has the highest CC, while *M. similis* Blume. in CBG has the lowest. The range value of CC for subgenus *Mangifera* species is 19.68 - 85.02 cci. *M. altissima* Blanco. has the highest SD, while *M. merrillii* Mukherji has the lowest. The range value of SD for subgenus *Mangifera* species is 699.06 - 1444.97. *M. rufocostata* Kosterm. has the longest SL, while *M. gedebe* Miq. is the shortest. The range value of leaf SL for subgenus *Mangifera* species is 13.57- 23.09µm. *M. rufocostata* Kosterm. has the widest SW, while *M. laurina* Blume. in CBG has the narrowest. The range value of leaf SW for subgenus *Mangifera* species is 13.47 - 21.57 µm.

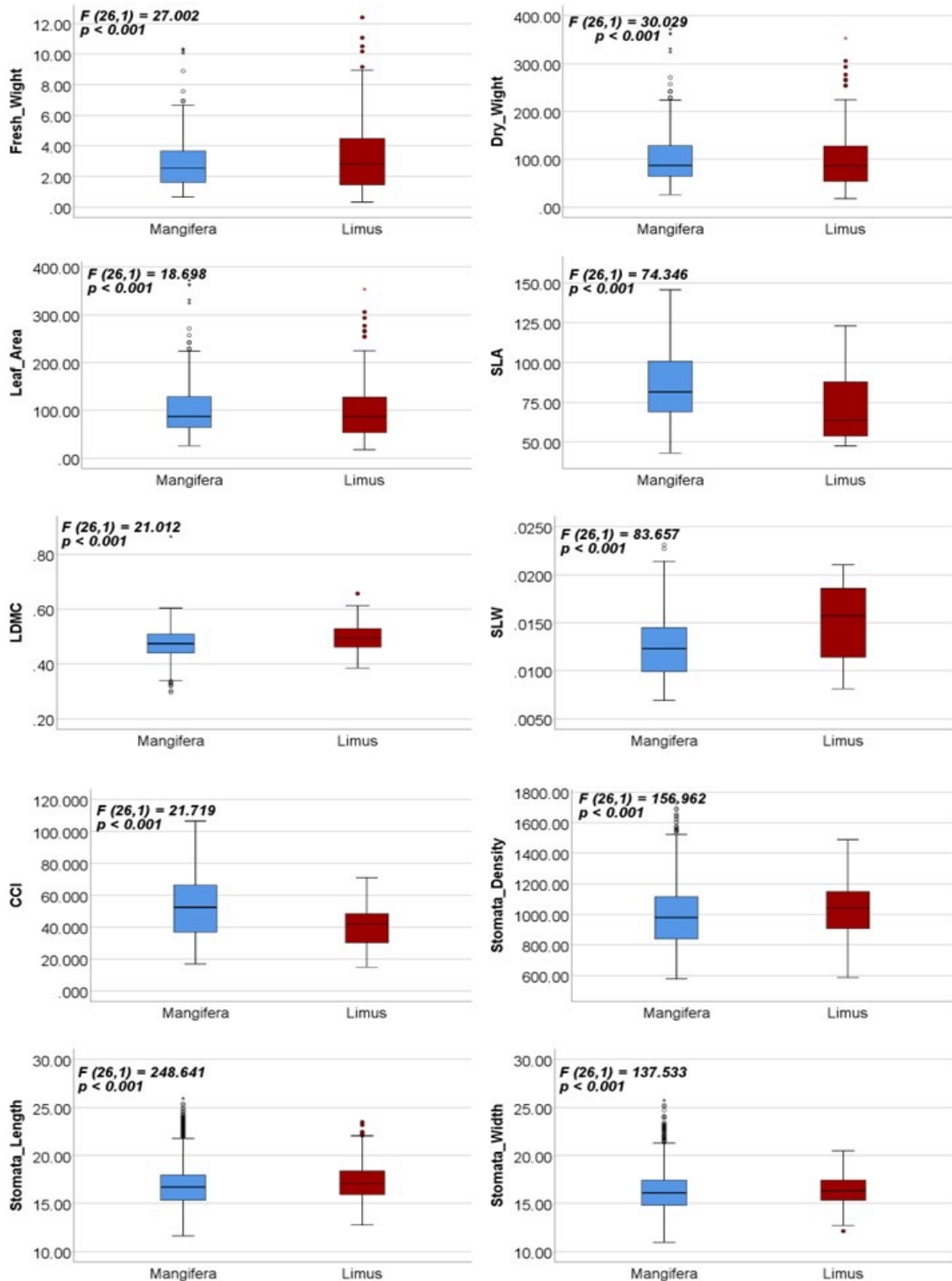


Figure 4. Boxplots of comparison of functional characters in various *Mangifera* species between subgenus *Mangifera* and *Limus*. Boxplots with significantly different colors at the $p = 0.05$ level

Table 1. Average differences in functional character values of *Mangifera* species within the subgenus *Mangifera*. Numbers followed by the same letter in the same column are not significantly different at $p = 0.05$.

Species	FW	DW	LA	SLA	SLW	LDMC	CC	SD	SL	SW
<i>Mangifera gedebe</i> Miq. (BBG)	1.25 ^a	0.57 ^a	56.06 ^a	98.66 ^g	0.0103 ^{bc}	0.46 ^{cde}	26.3 ^{ab}	1322.28 ^j	13.57 ^a	13.89 ^b
<i>Mangifera griffiti</i> Hook. (BBG)	3.68 ^{fg}	1.74 ^{de}	138.96 ^{efg}	79.69 ^{de}	0.0126 ^{ef}	0.48 ^{efg}	56.02 ^{def}	699.06 ^{cd}	17.73 ^{fg}	17.18 ^h
<i>Mangifera merrillii</i> Mukherji. (BBG)	1.89 ^{abcd}	0.95 ^{ab}	69.33 ^{ab}	72.10 ^{cd}	0.0137 ^{gh}	0.51 ^{fg}	72.14 ^g	992.90 ^a	18.37 ^g	16.39 ⁱ
<i>Mangifera indica</i> L. (BBG)	1.81 ^{abc}	0.92 ^{ab}	77.85 ^{abc}	86.19 ^{ef}	0.0118 ^{de}	0.51 ^{fg}	72.58 ^g	1067.97 ^{ef}	18.53 ^b	17.42 ^c
<i>Mangifera altissima</i> Blanco. (BBG)	3.73 ^{fg}	1.88 ^e	94.31 ^{abcde}	50.01 ^a	0.0200 ^j	0.50 ^{fg}	58.06 ^{ef}	1090.56 ^k	18.20 ^d	17.89 ^d
<i>Mangifera similis</i> Blume. (BBG)	4.16 ^g	2.38 ^f	147.38 ^{fg}	61.88 ^b	0.0162 ⁱ	0.57 ^h	41.8 ^c	1126.95 ^b	16.17 ^f	15.31 ^{ij}
<i>Mangifera similis</i> Blume. (CBG)	2.91 ^{cdef}	0.96 ^{ab}	110.83 ^{bcdef}	118.53 ⁱ	0.0086 ^a	0.33 ^a	19.68 ^a	1004.25 ^g	15.26 ^c	14.99 ^{cd}
<i>Mangifera torquenda</i> Kosterm. (BBG)	3.01 ^{defg}	1.33 ^{bcd}	121.48 ^{cdefg}	91.54 ^{fg}	0.0109 ^{cd}	0.44 ^{bcd}	36.66 ^{bc}	1116.0 ^g	16.49 ⁱ	16.01 ^j
<i>Mangifera applanata</i> Kosterm. (BBG)	2.33 ^{abcde}	1.01 ^{ab}	69.86 ^{ab}	69.06 ^{bc}	0.0145 ^h	0.43 ^{bc}	65.04 ^{fg}	737.11 ^g	23.09 ^h	21.57 ^k
<i>Mangifera casturi</i> Kosterm. (BBG)	2.8 ^{bcdef}	1.17 ^{bc}	131.34 ^{defg}	113.37 ^{hi}	0.0088 ^a	0.41 ^b	39.62 ^{cde}	1003.14 ^c	17.28 ^e	15.95 ^{fg}
<i>Mangifera oblingifolia</i> Hook. F. (BBG)	7.37 ^h	3.50 ^g	264.51 ^h	75.67 ^{cd}	0.0132 ^{fg}	0.47 ^{fg}	45.64 ^{cd}	914.31 ^{fg}	16.48 ^{hi}	15.58 ^{gh}
<i>Mangifera rufocostata</i> Kosterm. (BBG)	3.44 ^{efg}	1.79 ^{de}	93.04 ^{abcde}	52.98 ^a	0.0193 ^j	0.52 ^g	71.88 ^g	748.62 ^{ab}	17.33 ^j	17.52 ^l
<i>Mangifera pedicellata</i> Kosterm. (BBG)	3.66 ^{fg}	1.62 ^{cde}	159.67 ^g	97.81 ^g	0.0102 ^c	0.44 ^{bcde}	85.02 ^h	1099.41 ^{de}	20.45 ^e	17.13 ^e
<i>Mangifera minor</i> Blume. (BBG)	1.26 ^a	0.59 ^a	55.13 ^a	92.87 ^{fg}	0.0108 ^{cd}	0.47 ^{cdef}	28.66 ^{ab}	872.74 ^h	17.68 ^e	17.30 ^{ef}
<i>Mangifera laurina</i> Blume. (BBG)	2.39 ^{abcde}	1.21 ^{bc}	95.86 ^{abcde}	78.41 ^d	0.0126 ^{efg}	0.51 ^{fg}	60.54 ^{fg}	1056.84 ^{fg}	15.71 ^e	16.12 ^{gh}

There are diverse leaf functional traits among subgenus *Limus* (Table 2). *M. pajang* Kosterm. in BBG has the heaviest FW, while *M. foetida* Lour. in CBG is the lowest. The range value of leaf FW for subgenus *Limus* species is 0.57 g – 9.04 g. *M. pajang* Kosterm. in BBG has the heaviest DW, while *M. foetida* Lour. in CBG is the lowest. The range value of leaf DW for subgenus *Limus* species is 0.32 g – 4.79 g. *M. pajang* Kosterm. in BBG has the largest LA, while *M. foetida* Lour. in CBG is the smallest. The range value of LA for subgenus *Limus* species is 32.367 – 254.91 cm². *M. macrocarpa* Blume. in BBG has the highest SLA, while *M. pajang* Kosterm. in BBG has the lowest. The range value of SLA for subgenus *Limus* species is 53.403 – 111.819. *M. foetida* Lour. in CBG has the highest LDMC, while *M. ceasia* Jack ex Wall. in BBG has the lowest. The range value of LDMC for subgenus *Limus* species is 0.44 – 0.56. *M. foetida* Lour. W. S in BBG has the highest SLW, while *M. macrocarpa* Blume. in BBG is the lowest. The range value of SLW for subgenus *Limus* species is 0.09 – 0.19. *M. odorata* Giff. native range Jambi in CBG has the highest CC, while *M. foetida* Lour. in CBG is the lowest. The range value of CC for subgenus *Limus* species is 18.04 – 56.84 cci. *M. odorata* Griff. in BBG has the highest SD parameter, while *M. foetida* Lour. in CBG is the lowest. The range value of SD for subgenus *Limus* species is 824.85 – 1262.19. *M. pajang* Kosterm. in BBG has the longest SL, while *M. odorata* Giff. native range Java in CBG is the shortest. The range value of SL for subgenus *Limus* species is

15.12 – 20.45µm. *M. odorata* Griff. in BBG has the widest SW, while *M. odorata* Giff. native range Java in CBG is the narrowest. The range value of SW for subgenus *Limus* species is 15.1 – 17.52µm.

Genetic factors, environmental conditions, and the interaction between them influence the differences in leaf functional traits between the subgenus *Mangifera* and *Limus*. Genetic factors include species differences, genetic variation, and plant life strategies that determine growth rates and environmental adaptation. Pereira & Des Marais (2019) state that plant functional traits have a strong genetic basis and are crucial in plant-environment interactions. Genetic variation affects functional traits such as stomatal patterns, water use efficiency, and tolerance to environmental stress. Additionally, the evolution of plant functional traits is shaped by natural selection pressures from environmental factors, including climate change, resource availability, light intensity, soil nutrients, temperature, and biotic pressures, all contributing to functional trait variation. This is also supported by Hofhansl et al. (2021), who found that variations in leaf traits, such as leaf area, are influenced by environmental factors such as light availability and nutrient supply. Phenotypic plasticity, the outcome of the interplay between genetic and environmental factors, enables plants to modify their traits in response to environmental changes. Different functional leaf traits result from how plants develop and adapt within an ecosystem, which is determined by combining several elements.

Table 2. Average differences in functional character values of *Mangifera* species within subgenus *Limus*. Numbers followed by the same letter in the same column are not significantly different at $p = 0.05$

Species	FW	DW	LA	SLA	SLW	LDMC	CC	SD	SL	SW
<i>Mangifera foetida</i> Lour. S.K (BBG)	3.53 ^c	1.83 ^d	100.81 ^c	55.41 ^a	0.018 ^c	0.52 ^c	32.98 ^b	879.49 ^f	17.44 ^c	16.58 ^{ab}
<i>Mangifera foetida</i> Lour. W.S (BBG)	4.44 ^c	2.11 ^{de}	114.24 ^c	53.83 ^a	0.018 ^c	0.47 ^b	48.3 ^{cd}	954.41 ^c	14.51 ^d	14.75 ^{cd}
<i>Mangifera foetida</i> Lour. W.J (BBG)	3.67 ^c	1.72 ^{cd}	109.67 ^c	64.77 ^{bc}	0.016 ^{cd}	0.46 ^{ab}	50.2 ^{cd}	971.23 ^{de}	16.45 ^f	16.04 ^e
<i>Mangifera pajang</i> Kosterm. (BBG)	9.04 ^e	4.79 ^f	254.91 ^e	53.40 ^a	0.019 ^e	0.53 ^{cd}	44.58 ^c	1444.97 ^{ef}	15.90 ^g	15.17 ^{ef}
<i>Mangifera ceasia</i> Jack ex Wall. (BBG)	5.58 ^d	2.45 ^c	168.39 ^d	70.24 ^c	0.014 ^c	0.44 ^a	46.4 ^c	843.11 ^b	18.63 ^{de}	18.60 ^e
<i>Mangifera macrocarpa</i> Blume. (BBG)	1.41 ^{ab}	0.63 ^{ab}	69.16 ^b	111.82 ^f	0.009 ^a	0.44 ^a	31.4 ^{cd}	1262.55 ^d	17.44 ^b	17.53 ^d
<i>Mangifera odorata</i> Griff. (BBG)	1.85 ^b	0.94 ^b	59.45 ^{ab}	62.48 ^b	0.016 ^d	0.51 ^c	47.48 ^b	1081.25 ^h	16.35 ^d	15.86 ^e
<i>Mangifera odorata</i> Giff. (CBG) ^a	2.19 ^b	1.21 ^{bc}	67.33 ^b	56.39 ^a	0.018 ^c	0.55 ^{de}	30.42 ^b	1182.98 ^g	15.12 ^a	15.10 ^a
<i>Mangifera odorata</i> Giff. (CBG) ^b	1.34 ^{ab}	0.65 ^{ab}	57.71 ^{ab}	89.52 ^d	0.011 ^b	0.48 ^b	56.84 ^d	863.21 ^b	16.22 ^c	15.58 ^{bc}
<i>Mangifera foetida</i> Lour (CBG)	0.58 ^a	0.32 ^a	32.36 ^a	100.42 ^c	0.010 ^{ab}	0.56 ^c	18.04 ^a	824.85 ^a	17.85 ^e	16.85 ^e

Comparison of Functional Traits of *Mangifera* Species found in both Lowland and Highland Areas

Each species has different functional trait differences in lowland and highland (Table 3). Based on the differences in the average values of functional traits of the same *Mangifera* species at the lowland (BBG) and the highland (CBG), it is found that for *M. similis* Blume, the average values of FW, LA, SL, and SW do not significant differences except DW, SLW, SLA, LDMC, CC, and SD. The average values of DW and LA of *M. laurina* Blume. did, not show significant differences except DW, SLW, SLA, LDMC, CC, SD, SL, and SW. In *M. foetida* Lour., only the average value of SL is not a significant difference. Meanwhile, in *M. odorata* Griff., the average values of DW, LA, SLW, SLA, LDMC, and CC are insignificant, except for SD, SL, and SW.

According to Aryani et al. (2022), the altitude of plants habitat influences the differences of their functional traits due to the variety of air temperature, humidity, and light intensity. e Silva (2024), mentions that plants found in lowland areas have high SLA values. In *M. similis* Blume., *M. laurina*

Blume., *M. foetida* Lour., and *M. odorata* Griff., the average SLA values are higher in highland (CBG) compared to lowland (BBG). For *M. odorata* Griff., there were no significant differences in SLA between lowland and highland, indicating that this trait is less plastic in this species. According to Jahdi & Bussotti (2020) and Guo et al. (2018), the high SLA values in highland areas are caused by lower temperatures, more intense solar radiation, and shorter growing periods, which can drive plants to increase SLA to maximize the absorption of light for photosynthesis. Higher SLA allows leaves to be thinner with a larger surface area relative to their mass, supporting efficient light capture and growth. Highland plants often adapt to stressful conditions such as strong winds and low soil moisture. Increased SLA may reflect a strategy to enhance photosynthetic efficiency under limiting environmental conditions (Pan et al., 2013). Highland plants with higher SLA may exhibit high phenotypic plasticity, producing thin leaves with high SLA in response to environmental conditions such as increased temperature or changes in light.

Table 3. Differences in the average functional character values of *Mangifera* species were found in Bogor Botanical Gardens (BBG) and Cibodas Botanical Gardens (CBG).

Species	Location	Mean FW	Mean DW	Mean LA	Mean SLW	Mean SLA	Mean LDMC	Mean CC	Mean SD	Mean SL	Mean SW
<i>Mangifera similis</i>	BBG	4.156	2.381	147.385	0.016	61.884	0.574	41.8	748.62	17.33	17.52
	CBG	2.911	0.958	110.830	0.008	118.536	0.326	19.68	1004.25	15.26	15.00
	statistic	p > 0.05	p < 0.01	p > 0.05	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p > 0.05	p > 0.05
<i>Mangifera laurina</i>	BBG	2.393	1.207	95.855	0.013	78.411	0.511	60.54	971.24	16.45	16.04
	CBG	1.687	0.803	85.067	0.009	107.189	0.476	44.08	1182.87	13.73	13.47
	statistic	p > 0.05	p < 0.05	p > 0.05	p < 0.01	p < 0.01	p < 0.05	p < 0.05	p < 0.01	p < 0.01	p < 0.01
<i>Mangifera foetida</i>	BBG	3.880	1.886	108.241	4.059	58.003	0.487	43.83	1066.02	17.33	16.23
	CBG	0.579	0.317	32.368	0.010	100.417	0.564	18.04	824.85	17.85	16.85
	statistic	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p > 0.05	p < 0.05
<i>Mangifera odorata</i>	BBG	1.851	0.943	59.448	0.016	62.482	0.510	47.48	1262.55	17.44	17.56
	CBG	1.764	0.928	62.525	0.015	72.957	0.518	43.63	1023.1	15.67	15.34
	statistic	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p < 0.01	p < 0.01	p < 0.01

The diversity of leaf functional traits in *Mangifera* species found in lowland (BBG) and highland (CBG) areas can serve as criteria for selecting parent plants for *Mangifera* plant breeding. Plant breeding is a method that utilizes the genetic potential of plants to produce, select, and improve superior plant phenotypes to develop superior plant varieties (Singh et al., 2018). Plant breeding aims to identify and develop superior individuals and families. *M. indica* L. and *M. odorata* Giff. in CBG exhibit similar functional traits, thus these species could be recommended for plant breeding. The similar functional traits of *M. indica* L. and *M. odorata* Giff. in CBG can guide the breeding of new varieties; however, the compatibility between varieties needs further study, as differences in chromosome numbers and genome sizes may prevent direct genetic exchange between chromosomes.

CONCLUSION

The widespread distribution of *Mangifera* species affects their functional and phenotypic characteristics, reflecting their adaptation to different environments. There is a significant diversity in the functional traits of *Mangifera* species within the subgenus *Mangifera* and *Limus* due to the environmental factors that drive changes in phenotypic traits through plasticity and evolution. In the subgenus *Mangifera*, *M. similis* Blume in CBG has the highest SLA, *M. similis* Blume in BBG has the highest LDMC, and *M. altissima* Blanco. has the highest SLW. In the subgenus *Limus*, *M. macrocarpa* Blume has the highest SLA, *M. foetida* Lour. W. S in BBG has the highest SLW. It was found that the values of DW, LA, SLA, and CC are higher in the *Mangifera* subgenus compared to the *Limus* subgenus. The research also shows that the values of SLW, SLA, LDMC, and CC are influenced by altitude. The

diversity of functional traits in *Mangifera* species leaves found in lowland and highland areas can serve as criteria for selecting parent plants for cultivation breeding programs.

AUTHOR CONTRIBUTION

F.A. methodology, collected samples, data analysis, curation, and writing the original draft. **K.** conceptualization, methodology, data analysis and curation, investigation, supervised all the process. **V.K.** conceptualization designed the research, methodology, and data curation, wrote the original draft, reviewed a manuscript, and supervised all the processes. **W.R.** conceptualization designed the research, and data analysis, reviewed a manuscript, and supervised all the processes. **S.N.** conceptualization, methodology, and data analysis.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest regarding the publication of this manuscript. The research was conducted and reported with full adherence to ethical standards and without any financial or personal conflicts that could have influenced the results or interpretation.

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