

Phenotypic variation of African locust bean (*Parkia biglobosa*) across size classes in Côte d'Ivoire

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Abstract

Parkia biglobosa, "African locust bean" is a multipurpose savannah tree species of considerable socio-economic and cultural importance across West Africa. This study evaluated phenotypic diversity within three natural populations in Côte d'Ivoire using 13 morphological descriptors for individuals exceeding 5 cm diameter at breast height. Univariate and multivariate analyses examined intra- and inter-population variability across diameter classes. Results demonstrated substantial variation in dendrometric traits within sites, whilst foliar characteristics exhibited lower variability across developmental stages. Analysis of variance revealed significant differences amongst stands for eight parameters. Although dendrometric variables distinguishing size classes varied between sites, four foliar traits consistently differentiated them across all developmental stages. Multifactorial analyses indicated that expression of discriminant traits, particularly dendrometric parameters, intensified with tree age, reflecting increased morphological variation amongst size classes. Distinct morphological groups were identified at all developmental stages, irrespective of geographical distance, suggesting underlying genetic or ecological relationships. These groups were primarily distinguished by foliar characteristics. This research provides essential baseline data for selection, conservation, and domestication programmes targeting *P. biglobosa*, whilst contributing to enhanced sustainable management of this valuable agroforestry resource.

1. Introduction

Morphological variation in plant resources is the result of from the interaction between genetic and environmental factors, which collectively shape their phenotypes (Houehanou et al., 2019; Donhouédé et al., 2023). The evaluation of such variations can be achieved through the analysis of the characteristics exhibited by both vegetative and reproductive structures. The assessment of species within these categories provides the foundation for both domestication and forest management (Houehanou et al., 2019), an approach widely applied in tropical ecosystems. In sub-Saharan Africa, this strategy has become particularly urgent in savannah ecosystems, where increasing anthropogenic pressures, desertification, and climate change are driving significant ecological transformations (Kilroy, 2015). A substantial body of research has demonstrated that these disturbances have a direct impact on plant morphology, particularly in species with high socio-economic importance (Abdulai et al., 2017; Houehanou et al., 2019).

African locust bean (*Parkia biglobosa*), a species endemic to sub-Saharan Africa, is a multipurpose fruit tree that provides both woody and non-woody resources that are essential to local livelihoods (Nyadanu et al., 2017). The seeds are consumed on a daily basis and represent a significant source of income through regional trade (Vodouhê et al., 2011). The vitamin-rich pulp is also highly appreciated and consumed either raw or as a beverage (Koura et al., 2011). Moreover, various parts of the plant are used in traditional medicine for the treatment of numerous ailments (Dedehou et al., 2016). As a member of the Fabaceae family, *P. biglobosa* also contributes to soil fertility, thereby improving crop yields in agroforestry systems (Koura et al., 2011). However, the species' significant socio-economic value

exposes it to considerable anthropogenic pressure (Houndonougbo et al., 2020). Systematic fruit harvesting has been demonstrated to impede natural regeneration, while the ageing of existing stands contributes to population decline. In order to provide a robust foundation for the domestication of *P. biglobosa*, it is imperative to develop a comprehensive understanding of its natural variability, particularly given its wide geographic distribution. However, the evolution of morphological traits during tree development remains a relatively under-researched field, despite its critical importance for the assessment of species adaptation to environmental change. Furthermore, numerous studies have established correlations between morphological variation and geographical origin in plant species (Diggle, 2002; Fritz et al., 2018; Leal-Sáenz et al., 2020). In Côte d'Ivoire, *P. biglobosa* is present across various agroecological savannah zones and is recognized by local populations as one of the region's most valuable tree species (Ambe, 2001). Previous studies have identified three distinct morphological groups distributed along a south–north gradient (Kouonon et al., 2020). Nevertheless, analysis of the evolution of morphological traits evolve during tree development is essential for a deeper understanding of forest community dynamics. According to Barton (2024) posited that trait variation is partly attributable to ontogenesis, that is, the progressive increase in plant size and age. Despite the paucity of research in this area, this perspective constitutes a fundamental element of sustainable forest resource management, particularly in the context of African fruit trees.

This study therefore aims to characterise the morphological variability in *P. biglobosa* across several age classes in Côte d'Ivoire, with a focus on supporting domestication and sustainable conservation efforts. Specifically, the objectives were: (i) to determining the phenotypic diversity between three natural stands based on diameter classes, (ii) to characterize the structure of this variability within the different diameter classes, and (iii) to identify homogeneous morphological groups and determine the key traits that distinguish them.

2. Material and Methods

2.1. Target Species and study area

This study focused on African locust bean (*P. biglobosa*), a West African agroforestry fruit species of significant socio-economic importance. In Côte d'Ivoire, *P. biglobosa* is predominantly distributed across savannah agroecological zones. Three stands were selected along a south-north climatic gradient, each representing a distinct savannah ecosystem. A comprehensive set of soil data for these sites was obtained from the Global Soil Grids database (<https://soilgrids.org/>) (Hengl et al., 2017).

Koumokro stand (Guinean savannah zone)

The Koumokro stand is located in the Bocanda department (N'Zi region, central Côte d'Ivoire), within the forest–savannah transition zone. The region is characterised by a humid tropical climate, with an average annual rainfall of approximately 1043 mm and mean temperatures ranging between 25 and 29°C (Koita et al., 2010; Fossou et al., 2014, 2020). The climate is bimodal, characterized by two rainy and two

dry seasons (Fossou et al., 2014). The vegetation is dominated by a of shrubby savannah. The soils are predominantly alluvial and hydromorphic, exhibiting a general tendency towards acidity and significant weathering, accompanied by pronounced leaching. The location of the site is of particular ecological interest, being situated along a river that experiences flooding during the rainy season. Human and animal disturbance is a significant concern due to the presence of nearby settlements and subsistence crop cultivation.

Kouassi-N'Dawa stand (sub-sudanese savannah zone)

The stand of Kouassi-N'Dawa is situated within the Bondoukou department of north-eastern Côte d'Ivoire. The region's climate is tropical and humid, with two rainy and two dry seasons. The annual rainfall range is between 800 and 1200 mm, with a mean temperature of approximately 28°C (Brou et al., 2005; Kouman et al., 2024). The vegetation of this region exhibits characteristics that are transitional between those of forest and savannah ecosystems. Human activity is marked by the extensive cultivation of cashews, while pastoralism is minimal. The landscape is characterised by gallery forests interspersed with cashew fields and savannah trees, bordered by the Bayakokoré river. The region is also subject to mineral extraction activities. The topography is characterised by moderate undulations, and the soils are acidic and have undergone extensive weathering.

Pouniakélé site (sudanese savannah zone)

The Pouniakélé's site, situated in the Bagoué region of northern Côte d'Ivoire, falls within the Sudanese climatic zone, which is distinguished by the presence of two clearly defined seasons. The annual rainfall varies from 1000 to 1400 mm, and the mean temperature averages 27°C (Silue et al., 2023). Vegetation consists of light forests and open savannahs (Ouattara et al., 2016). The soils are predominantly ferrallitic, with clay horizons that restrict water infiltration and mechanical processes. The area forms part of a broad plateau, exhibiting minimal altitudinal variation (Silue et al., 2023). Anthropogenic pressures are pronounced, including bushfires, rural agriculture, and pastoral activities. The landscape is composed mainly of fallow lands interspersed with scattered trees, predominantly *P. biglobosa*, and bordered by extensive industrial crop plantations. The soils are sandy and fertile but prone to seasonal flooding.

2.2. Data collection

At each study site, *P. biglobosa* stands were identified and exhaustively inventoried (all trees with D1.30 $\geq$ 5 cm measured). Each stand was systematically surveyed by walking it in parallel paths to ensure complete coverage of its extent. The study focused on thirteen morphological descriptors measured across multiple organizational levels. Dendrometric traits included the diameter at 1.30 m (D1.30), measured with a diameter tape; bole height, defined as the distance from the ground to the first living branch; total height, measured using a graduated pole; and crown spread, calculated as the mean of two perpendicular canopy diameters. Foliar traits were assessed on five fully expanded leaves per tree, sampled from different crown aspects. For each leaf, we recorded total leaf length, maximum leaf width

(distance between the two outermost leaflets when flattened), petiole length, and the number of leaflets. On the terminal leaflet of each sampled leaf, we measured leaflet length and width, counted the number of pinnae, and measured both the length and width of the terminal pinna. For each tree, trait values were averaged across the five leaves.

2.3. Data processing and analysis

Trees were categorized into three size classes based on their diameter at breast height (DBH): young trees (5–15 cm), adult trees (15–45 cm), and old trees (> 45 cm), based on the observed diameter distribution and biological knowledge of reproductive maturity in *P. biglobosa*. For each size class, differences in morphological traits among the three sites were tested using one-way ANOVA or Welch's correction under heteroscedasticity, followed by Fisher's LSD or Games-Howell post hoc tests. Multivariate analyses were conducted for each size class. All variables were standardized before analysis. Data suitability was assessed using Kaiser-Meyer-Olkin ($KMO \geq 0.5$) and Bartlett's sphericity test. Principal Component Analysis (PCA) was applied to reduce dimensionality, retaining components explaining $\geq 70\%$ of total variance. Hierarchical Cluster Analysis (HCA) using Ward's method on principal component scores grouped trees by morphological similarity. Discriminant Function Analysis (DFA) identified the most discriminant traits among HCA-derived groups, using Wilks' Lambda and Mahalanobis distances. Finally, for each size class and group identified, means values were calculated to characterise morphological differences precisely. All statistical analyses were performed using XLSTAT software (version 2019).

3. Results

3.1. Comparison of the three stands of *P. biglobosa* based on the measured parameters

3.1.1 Young trees

Dendrometric parameters exhibited moderate to high variability ($19\% < CV < 46\%$), whereas foliar parameters showed low to moderate variability ($6\% < CV < 23\%$). Among the dendrometric traits, only the diameter exhibited a significant difference between the stands ($P < 0.05$). The highest mean diameter was recorded in Koumokro, followed by Pouniakélé, while the lowest value was observed in Kouassi-N'Dawa. For foliar parameters, significant differences between stands ($P < 0.05$) were observed for petiole length, number of leaflets, leaflet length and width, as well as the number and length of pinnae. In Koumokro, young trees exhibited elongated petioles and a greater number of leaflets. The leaflets were characterised by reduced length but greater width. Furthermore, the number of pinnae was found to be relatively low, and their length was found to be intermediate (Table 1).

Table 1

Mean values and coefficients of variance of morphological traits of *P. biglobosa* within the young trees

Variable (Cm)	Koumokro (N = 29)		Kouassi-N'Dawa (N = 22)		Pouniakélé (N = 13)		P
	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	
D _{1.30}	8.03 $\pm$ 1.51 ^a	19%	6.93 $\pm$ 1.47 ^b	21%	7.13 $\pm$ 1.45 ^{ab}	20%	0.028
Tbh	159.5 $\pm$ 54.35	34%	215.39 $\pm$ 97.39	45%	183.08 $\pm$ 84.11	46%	0.067
Tht	438.64 $\pm$ 95.47	22%	476.68 $\pm$ 139.72	29%	499.62 $\pm$ 98.02	20%	0.229
Tcs	227.55 $\pm$ 53.61	24%	241.08 $\pm$ 75.79	31%	279.3 $\pm$ 71.96	26%	0.088
Ptl	8.13 $\pm$ 1.24 ^a	15%	7.7 $\pm$ 0.62 ^a	8%	6.47 $\pm$ 1.23 ^b	19%	0.002
Lel	43.35 $\pm$ 5.46	13%	39.65 $\pm$ 4.59	12%	41.25 $\pm$ 7.62	18%	0.076
Lew	26.45 $\pm$ 3.53	13%	24.54 $\pm$ 3.31	13%	26.17 $\pm$ 3.11	12%	0.127
Len	23.96 $\pm$ 2.73 ^a	11%	21.82 $\pm$ 1.62 ^b	7%	24.12 $\pm$ 4.02 ^{ab}	17%	0.004
Tll	10.24 $\pm$ 1.43 ^b	14%	9.73 $\pm$ 1.17 ^b	12%	11.24 $\pm$ 1.6 ^a	14%	0.011
Tlw	2.38 $\pm$ 0.49 ^a	21%	2.47 $\pm$ 0.22 ^a	9%	2.11 $\pm$ 0.25 ^b	12%	0.029
Pn	62.95 $\pm$ 6.3 ^b	10%	58.01 $\pm$ 3.38 ^c	6%	78.35 $\pm$ 8.47 ^a	11%	< 0.001
Pl	0.8 $\pm$ 0.12 ^b	15%	0.96 $\pm$ 0.06 ^a	6%	0.68 $\pm$ 0.12 ^c	17%	< 0.001
Pw	0.25 $\pm$ 0.05	19%	0.25 $\pm$ 0.02	9%	0.22 $\pm$ 0.05	23%	0.133
(D1.30: Diameter at 1.30 m height); (Tbh: bole height of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); Different superscript letters indicate significant differences (p < 0.05)							

3.1.2 Adult trees

In adult trees, dendrometric variables exhibited substantial and statistically significant variability (22% $\leq$ CV $\leq$ 52%). Conversely, foliar variables exhibited lower to moderate variability (6% $\leq$ CV $\leq$ 22%). Among the dendrometric traits, two variables (diameter and bole height) significantly differentiated the stands. The largest mean diameter was recorded in Koumokro, followed by Kouassi-N'Dawa, while the smallest values were observed in Pouniakélé. In a similar manner, trees from Pouniakélé exhibited the lowest bole

heights, in contrast to the taller specimens in the other two stands. With regard to foliar traits, five parameters were identified as discriminant among stands: petiole length, leaflet width, number of pinnae, and pinnae length and width. The majority of adult trees from Kouassi-N'Dawa demonstrated the highest mean values for these characteristics, particularly for petiole length. In contrast, trees from Koumokro were distinguished by broader leaflets and a lower number of pinnae, which were nevertheless larger in size (Table 2).

Table 2
Mean values and coefficients of variance of morphological traits of *Parkia biglobosa* within the adult trees

Variable (Cm)	Koumokro (N = 86)		Kouassi-N'Dawa (N = 51)		Pouniakélé (N = 61)		P
	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	
D_{1.30}	22.22 $\pm$ 7.32 a	33%	20.03 $\pm$ 7.21 ab	36%	18.95 $\pm$ 6.45 b	34%	0.018
Tbh	284.12 $\pm$ 136.29 ^a	48%	299.31 $\pm$ 144.23 ^a	48%	204.12 $\pm$ 105.88 ^b	52%	0.000
Tht	781.4 $\pm$ 208.14	27%	785.82 $\pm$ 191.48	24%	822 $\pm$ 178.81	22%	0.430
Tcs	558.88 $\pm$ 215.65	39%	539.8 $\pm$ 242.27	45%	526.05 $\pm$ 196.97	37%	0.658
Ptl	7.16 $\pm$ 1.21 ^a	17%	7.26 $\pm$ 0.73 ^a	10%	6.26 $\pm$ 1.19 ^b	19%	< 0.001
Lel	37.15 $\pm$ 5.5	15%	37.29 $\pm$ 4.99	13%	36.56 $\pm$ 5.11	14%	0.722
Lew	23.73 $\pm$ 3.24	14%	23.88 $\pm$ 3.16	13%	24.2 $\pm$ 3.21	13%	0.684
Len	23.01 $\pm$ 2.62	11%	23.31 $\pm$ 1.75	8%	24.07 $\pm$ 2.9	12%	0.080
Tll	9.48 $\pm$ 1.42	15%	9.4 $\pm$ 1.03	11%	9.74 $\pm$ 1.58	16%	0.401
Tlw	2.19 $\pm$ 0.32 ^b	14%	2.36 $\pm$ 0.23 ^a	10%	1.92 $\pm$ 0.26 ^c	14%	< 0.001
Pn	63.52 $\pm$ 6.36 b	10%	59.45 $\pm$ 3.33 c	6%	76.2 $\pm$ 9.19 ^a	12%	< 0.001
Pl	0.73 $\pm$ 0.12 ^b	16%	0.96 $\pm$ 0.12 ^a	12%	0.64 $\pm$ 0.12 ^c	19%	< 0.001
Pw	0.23 $\pm$ 0.05 ^b	22%	0.26 $\pm$ 0.04 ^a	15%	0.21 $\pm$ 0.04 ^c	17%	< 0.001
(D _{1.30} : Diameter at 1.30 m height); (Tbh: Height of the bole of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); different superscript letters indicate significant differences (p < 0.05)							

3.1.3 Old trees

In the old-growth size class, dendrometric parameters had coefficients of variation ranging from fairly large to large. In contrast, foliar parameters showed lower variability, ranging from low to moderate levels ($8\% \leq CV \leq 21\%$). The differentiation of stands was primarily explained by two dendrometric variables: bole height and total height. The Pouniakélé stand recorded the lowest mean values for these parameters, whereas the Kouassi-N'Dawa and Koumokro stands exhibited the highest averages. Regarding foliar traits, trees from Pouniakélé were characterized by short petioles bearing large leaves composed of numerous thin leaflets. These leaflets, in turn, consisted of a large number of small pinnae (Table 3).

Table 3

Mean values and coefficients of variance of morphological traits Morphological variation of *Parkia biglobosa* within the old trees

Variable (Cm)	Koumokro (N = 47)		Kouassi-N'Dawa (N = 28)		Pouniakélé (N = 13)		P
	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	Mean $\pm$ SD	CV	
D _{1.30}	47.84 $\pm$ 11.77	25%	51.29 $\pm$ 11.09	22%	51.66 $\pm$ 16.76	32%	0.406
Tbh	303.62 $\pm$ 122.35 _a	40%	321.72 $\pm$ 119.78 _a	37%	142.54 $\pm$ 67.01 _b	47%	< 0.001
Tht	1267.21 $\pm$ 219.37 _a	17%	1430.58 $\pm$ 456.23 _a	32%	1089 $\pm$ 187 _b	17%	0.003
Tcs	1258.24 $\pm$ 404.49	32%	1307.43 $\pm$ 454.98	35%	1121.15 $\pm$ 521.61	47%	0.451
Ptl	6.96 $\pm$ 1.09 _b	16%	7.57 $\pm$ 1.19 _a	16%	5.9 $\pm$ 0.86 _c	15%	< 0.001
Lel	35.27 $\pm$ 4.23 _b	12%	35.46 $\pm$ 4.55 _a	13%	36.87 $\pm$ 4.19 _c	11%	0.494
Lew	23.03 $\pm$ 2.69 _b	12%	23.62 $\pm$ 2.49 _{ab}	11%	25.21 $\pm$ 3.35 _a	13%	0.043
Len	23.54 $\pm$ 2.8 _{ab}	12%	23.06 $\pm$ 2.66 _b	12%	25.52 $\pm$ 2.45 _a	10%	0.027
Tll	8.92 $\pm$ 1.07	12%	9.26 $\pm$ 1.06	11%	9.75 $\pm$ 1.47	15%	0.059
Tlw	2.19 $\pm$ 0.43 _a	20%	2.35 $\pm$ 0.4 _a	17%	1.92 $\pm$ 0.23 _b	12%	0.009
Pn	61.47 $\pm$ 6.09 _b	10%	59.4 $\pm$ 4.69 _b	8%	77.81 $\pm$ 8.24 _a	11%	< 0.001
Pl	0.71 $\pm$ 0.1 _b	14%	0.97 $\pm$ 0.11 _a	11%	0.63 $\pm$ 0.12 _b	18%	< 0.001
Pw	0.23 $\pm$ 0.04 _b	16%	0.27 $\pm$ 0.03 _a	12%	0.2 $\pm$ 0.04 _b	21%	< 0.001

(D_{1.30}: Diameter at 1.30 m height); (Tbh: Height of the bole of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); different superscript letters indicate significant differences ($p < 0.05$).

3.2. Structuring morphological variability

3.2.1 Young trees

Six morphological parameters (diameter at 1.30 m, bole height, total height, petiole length, leaf length, and number of leaflets) were excluded from the multivariate analyses due to KMO values below 0.5. However, the overall KMO index ($KMO > 0.5$) and Bartlett's test of sphericity ($\chi^2 = 42.212$; $df = 23$; $P < 0.001$) confirmed that the remaining variables were suitable for multifactorial analysis of the young tree size class. The HCA dendrogram revealed four distinct groups (Fig. 1A). Groups 1 and 2 comprised individuals originating from all three provenances, with trees from Kouassi-N'Dawa representing 68% and 69% of these groups, respectively. In contrast, Groups 3 and 4 were composed primarily of individuals from Koumokro and Pouniakélé, respectively. Group 3 contained predominantly trees from Pouniakélé (56% of the total population) and 44% from Koumokro, while Group 4 was dominated by trees from Koumokro (71%) and included 29% from Pouniakélé (Fig. 1B). [Insert Fig. 1]

The four previous group classification was confirmed by the FDA ($\Lambda = 0.127$, $F = 10.442$, $P < 0.001$), with the groups projected according to the explanatory variables in the 1–2 factorial plane (Fig. 2). Pairwise comparisons using Mahalanobis distances were all statistically significant. The most significant separation was observed between Groups 2 and 4 ($D^2 = 86.743$), whereas Groups 1 and 3, and Groups 1 and 2, were the closest, with distances of 10.419 and 14.43, respectively. The distances between the remaining pairs of groups were intermediate. [Insert Fig. 2]

Eight of the thirteen variables were identified as significantly discriminant among the groups within the young tree size class. The traits that exhibited the greatest discriminatory power were pinnae length and width, in that order (Table 4). Group 3 demonstrated the lowest mean values for the majority of the descriptors. Among the dendrometric parameters, only crown spread differed significantly between the groups, with trees in Group 3 displaying the largest crown spread. With regard to foliar traits, all variables except the number of leaflets demonstrated significant differences among the groups. The highest mean values were generally observed in Group 2, with the exception of the number of pinnae.

Table 4

Quantitative traits variation following the groups of *Parkia biglobosa* trees within the young trees

Variables (Cm)	C1 (N = 28) Mean ± SD	C2 (N = 13) Mean ± SD	C3 (N = 16) Mean ± SD	C4 (N = 7) Mean ± SD	Pr	λ
D _{1.30}	7.21 ± 1.40	7.56 ± 1.91	7.34 ± 1.55	8.66 ± 1.09	0.165	0.919
Tbh	191.54 ± 140.74	167.23 ± 82.99	190.69 ± 100.488	165.14 ± 88.731	0.736	0.979
Tht	465.46 ± 140.74	458.38 ± 82.99	472.47 ± 100.488	450.14 ± 88.731	0.974	0.996
Tcs	236.82 ± 65.99 ^{ab}	199.24 ± 37.20 ^b	266.95 ± 67.7 ^a	291.60 ± 73.9 ^a	0.007	0.820
Ptl	7.69 ± 0.8 ^{ab}	8.30 ± 1.02 ^a	7.51 ± 1.74 ^{ab}	6.54 ± 0.92 ^b	0.017	0.846
Lel	39.84 ± 4.61 ^{bc}	46.83 ± 5.38 ^a	42.86 ± 5.85 ^{ab}	36.53 ± 3.32 ^c	< 0.001	0.698
Lew	24.49 ± 2.79 ^b	29.29 ± 2.68 ^a	26.77 ± 2.11 ^a	21.74 ± 2.70 ^b	< 0.001	0.548
Len	22.64 ± 2.39	23.58 ± 3.37	23.55 ± 3.3	24.46 ± 2.91	0.428	0.955
Tll	9.6 ± 0.84 ^b	11.52 ± 1.01 ^a	11.25 ± 1.23 ^a	8.34 ± 1.09 ^c	< 0.001	0.450
Tlw	2.42 ± 0.18 ^b	2.76 ± 0.50 ^a	2.12 ± 0.21 ^c	1.87 ± 0.12 ^c	< 0.001	0.503
Pn	59.5 ± 4.29 ^b	61.17 ± 5.12 ^b	75.49 ± 9.67 ^a	64.45 ± 10.88 ^{ab}	< 0.001	0.513
Pl	0.91 ± 0.08 ^a	0.93 ± 0.07 ^a	0.70 ± 0.08 ^b	0.61 ± 0.09 ^c	< 0.001	0.303
Pw	0.25 ± 0.02 ^a	0.28 ± 0.04 ^{ab}	0.22 ± 0.04 ^b	0.18 ± 0.02 ^c	< 0.001	0.548
(D _{1.30} : Diameter at 1.30 m height); (Tbh: Height of the bole of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); different superscript letters indicate significant differences (p < 0.05)						

3.2.2 Adult trees

The Bartlett's test of sphericity ($P < 0.001$), in conjunction with KMO, enabled the selection of ten variables suitable for multifactorial analysis at a threshold of 0.5. The following variables were considered: diameter at 1.30 m, total height, crown spread, petiole length, leaf length, leaf width, leaflet length, leaflet width, and pinnae length and width.

The HCA results enabled the classification of adult trees from all provenances into four distinct morphogroups (Fig. 3A & B). Group 1 constituted 23% of the adult population, with the majority of trees (47%) originating from Koumokro and 42% from Kouassi-N'Dawa. Morphogroup 2 constituted 23% of the population, with a preponderance of trees from Koumokro (46%) and Pouniakélé (48%). Group 3 comprised trees from all three stands, with 41%, 32%, and 27% of individuals originating from Koumokro, Pouniakélé, and Kouassi-N'Dawa, respectively. [Insert Fig. 3]

The DFA performed on the ten variables derived from the morphological groups identified by hierarchical classification revealed a highly significant differentiation among groups ($\Lambda = 0.093$; $F = 22.623$; $P < 0.001$). The projection of individuals in the factorial plane of the discriminant analysis is presented in Fig. 4. Pairwise comparisons of Mahalanobis distances between groups were all statistically significant. Groups 2 and 3 were the closest ($D^2 = 8.318$), whereas Groups 4 and 2 were the most distant ($D^2 = 26.335$). Intermediate distances were observed between Groups 1 and 3 ($D^2 = 12.323$), 1 and 4 ($D^2 = 12.406$), and 4 and 3 ($D^2 = 10.636$) [Insert Fig. 4].

All measured variables, except the number of leaflets, were found to be significantly discriminant within the adult tree. According to Wilks' partial Lambda values, the most discriminating traits were tree diameter, crown spread, leaf length, leaf width, and leaflet length and width (Table 5). Group 1 exhibited the highest mean values for dendrometric parameters. In contrast, Group 3 displayed the lowest values for all these parameters. With regard to foliar traits, Group 4 exhibited the highest mean values, while Group 2 demonstrated the lowest. Trees in Group 4 were distinguished by their long, broad leaves supported by elongated petioles. The leaflets of this group exhibited the greatest dimensions and the highest number of pinnae. The pinnae themselves demonstrated the greatest dimensions.

Table 5
Quantitative traits variation following the groups of *P. biglobosa* trees within the adult trees

Variables (Cm)	C1 (N = 45)	C2(N = 46)	C3(N = 78)	C4(N = 29)	P	λ
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD		
D_{1.30}	29.03 $\pm$ 4.69 ^a	22.49 $\pm$ 5.34 ^b	15.29 $\pm$ 3.9 ^b	19.14 $\pm$ 6.02 ^c	< 0.001	0.441
Tbh	318.44 $\pm$ 168.93 ^a	242.2 $\pm$ 118.26 ^b	250.79 $\pm$ 118.11 ^b	245.42 $\pm$ 129.69 ^b	0.020	0.950
Tht	956.58 $\pm$ 206.56 ^a	848.11 $\pm$ 147.46 ^b	673.60 $\pm$ 138.90 ^c	786.86 $\pm$ 158.25 ^b	< 0.001	0.672
Tcs	776.26 $\pm$ 182.78 ^a	607.25 $\pm$ 162.46 ^b	382.85 $\pm$ 98.9 ^c	515.68 $\pm$ 205.62 ^b	< 0.001	0.496
Ptl	6.87 $\pm$ 0.8 ^b	6.01 $\pm$ 1.08 ^c	7.02 $\pm$ 0.96 ^b	8.1 $\pm$ 1.25 ^a	< 0.001	0.711
Lel	34.94 $\pm$ 3.44 ^c	32.949 $\pm$ 3.89 ^d	37.99 $\pm$ 3.85 ^b	43.96 $\pm$ 4.75 ^a	< 0.001	0.551
Lew	22.97 $\pm$ 2.6 ^c	20.99 $\pm$ 2.36 ^d	24.67 $\pm$ 2.51 ^b	27.98 $\pm$ 2.53 ^a	< 0.001	0.524
Len	23.12 $\pm$ 2.53	23.57 $\pm$ 2.76	23.48 $\pm$ 2.41	23.47 $\pm$ 2.71	0.848	0.996
Tll	9.12 $\pm$ 0.80 ^c	8.28 $\pm$ 0.89 ^d	9.83 $\pm$ 1.08 ^b	11.23 $\pm$ 1.44 ^a	< 0.001	0.559
Tlw	2.2 $\pm$ 0.25 ^b	1.84 $\pm$ 0.21 ^c	2.14 $\pm$ 0.24 ^b	2.55 $\pm$ 0.28 ^a	< 0.001	0.554
Pn	62.87 $\pm$ 7.14 ^b	65.61 $\pm$ 9.17 ^{ab}	68.15 $\pm$ 10.6 ^a	68.28 $\pm$ 9.43 ^a	0.016	0.949
Pl	0.82 $\pm$ 0.16 ^{ab}	0.61 $\pm$ 0.1 ^c	0.77 $\pm$ 0.16 ^b	0.87 $\pm$ 0.14 ^a	< 0.001	0.734
Pw	0.234 $\pm$ 0.036 ^b	0.192 $\pm$ 0.037 ^c	0.243 $\pm$ 0.048 ^{ab}	0.259 $\pm$ 0.039 ^a	< 0.001	0.763

(D_{1.30}: Diameter at 1.30 m height); (Tbh: Height of the bole of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); different superscript letters indicate significant differences ($p < 0.05$)

3.2.3 Old trees

Bartlett's test of sphericity ($P < 0.001$) and the KMO analysis confirmed that all variables were suitable for multifactorial analysis at the 0.5 threshold in this size class. The HCA identified three distinct

morphological groups among the old trees (Fig. 5A). Groups 1 and 2 were exclusively comprised of individuals from Koumokro and Kouassi-N'Dawa, respectively. Conversely, Group 3 comprised trees from both Koumokro and Pouniakélé, with the majority of these originating from Pouniakélé (Fig. 5B). [Insert Fig. 5]

The DFA results confirmed the group structure obtained from the hierarchical clustering for the old tree ($\Lambda = 0.079$; $F = 14.344$; $P < 0.001$). The patterns distribution of the groups in the factorial plane is presented in Fig. 6. All Mahalanobis distances calculated between groups were statistically significant. The smallest distance ($D^2 = 6.906$) was observed between Groups 2 and 3, indicating a closer morphological resemblance, while the largest distance ($D^2 = 30.996$) occurred between Groups 1 and 3. Groups 1 and 2 were separated by an intermediate distance of 12.307. [Insert Fig. 6]

All measured variables significantly differentiated the groups in the old tree. The univariate test demonstrated that the number of pinnae and total tree height exhibited the greatest discriminatory power (Table 6). Group 1 recorded the highest mean values for dendrometric parameters, comprising trees with the largest diameters, the tallest bole, the greatest total heights, and the widest crowns. Conversely, Group 3 was distinguished by its superior foliar dimensions, displaying the highest average leaf traits. Trees in this group possessed large leaves borne on short petioles. The leaves were found to comprise a high number of leaflets that are long and narrow. The pinnae are relatively large and numerous.

Table 6
Quantitative traits variation following the groups of *P. biglobosa* trees within the old trees

Variables (Cm)	C1 (N = 29)	C2 (N = 44)	C3 (N = 15)	Pr	λ
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD		
D_{1.30}	57.93 $\pm$ 11.26 ^a	43.13 $\pm$ 7.38 ^b	51.90 $\pm$ 15.847 ^a	< 0.001	0.705
Tbh	320.93 $\pm$ 102.41 ^a	306.61 $\pm$ 134.17 ^a	155.53 $\pm$ 70.99 ^b	< 0.001	0.786
Tht	1606.38 $\pm$ 302.41 ^a	1153.87 $\pm$ 219.95 ^b	1094.47 $\pm$ 173.90 ^b	< 0.001	0.541
Tcs	1573.71 $\pm$ 452.61 ^a	1075.21 $\pm$ 264.93 ^b	1158.27 $\pm$ 494.85 ^b	< 0.001	0.730
Ptl	7.53 $\pm$ 1.20 ^a	6.98 $\pm$ 1.10 ^b	6.02 $\pm$ 0.91 ^c	0.000	0.821
Lel	36.58 $\pm$ 4.79 ^a	34.32 $\pm$ 3.75 ^b	37.25 $\pm$ 4.07 ^a	0.021	0.913
Lew	24.48 $\pm$ 2.79 ^a	22.35 $\pm$ 2.15 ^b	25.22 $\pm$ 3.14 ^a	0.000	0.811
Len	22.05 $\pm$ 2.93 ^c	24.03 $\pm$ 2.2 ^b	25.78 $\pm$ 2.42 ^a	< 0.001	0.780
Tll	9.39 $\pm$ 1.24 ^a	8.77 $\pm$ 0.85 ^b	9.80 $\pm$ 1.44 ^a	0.004	0.878
Tlw	2.48 $\pm$ 0.46 ^a	2.1 $\pm$ 0.33 ^b	1.95 $\pm$ 0.28 ^b	< 0.001	0.758
Pn	58.27 $\pm$ 5.77 ^c	61.61 $\pm$ 4.28 ^b	77.52 $\pm$ 7.66 ^a	< 0.001	0.395
Pl	0.89 $\pm$ 0.16 ^a	0.75 $\pm$ 0.14 ^b	0.63 $\pm$ 0.12 ^c	< 0.001	0.702
Pw	0.25 $\pm$ 0.04 ^a	0.23 $\pm$ 0.03 ^b	0.22 $\pm$ 0.06 ^b	0.005	0.883

(D_{1.30}: Diameter at 1.30 m height); (Tbh: Height of the bole of tree); (Tht: Total height of tree); (Tcs: crown spread of tree); (Ptl: Petiole length); (Tll: Total leaf length); (Tlw: Total leaf width); (Len: Number of leaflets); (Lel: Leaflet length); (Lew: Leaflet width); (Pn: Number of pinnae); (Pl: Pinnae length); (Pw: Pinnae width); (N: Number of trees); Different superscript letters indicate significant differences (p < 0.05).

4. Discussion

Across the three size classes, dendrometric traits displayed strong within-site variation, reflecting marked phenotypic plasticity and sensitivity to local environmental heterogeneity. Such flexibility enhances the

species' adaptive potential under variable ecological conditions. In contrast, the lower variability of foliar traits suggests functional constraints linked to photosynthesis, water balance, and gas exchange, which limit their range of morphological adjustment while ensuring physiological efficiency (Azmat et al., 2020).

Of the stands studied, Koumokro exhibited the most favourable dendrometric characteristics, which remained discriminant across all developmental stages. In young trees, inter-stand variations were primarily evident in trunk diameter, with significant variability observed among sites. This phenomenon can be attributed to the high sensitivity of diameter growth to stand dynamics during the early development stage. The absence of significant variation in other dendrometric characteristics could be attributed to their strong correlation with diameter and the predominance of radial growth at this stage. The elevated values recorded in Koumokro are likely indicative of optimal access to nutrients, reduced competition among individuals, or silvicultural conditions that limit disturbance. The deep, well-structured soils characteristic of this site further provides favourable edaphic conditions for growth. In mature trees, trunk diameter and total height were found to be the principal discriminant dendrometric traits, suggesting that ecological contrasts among sites become more pronounced with age. These traits are indicative of individual vigour and competitiveness, reflecting an ontogenetic shift towards intensified radial expansion and vertical allometry as competition for light and biomass accumulation increases (Chave et al., 2009). The findings indicate that Koumokro's sustained dominance in diameter growth is indicative of the stand's ability to consistently maintain optimal ecological conditions conducive to continuous radial development, a process that is known to favour individuals exhibiting early growth plasticity (Poorter et al., 2005). The elevated bole height recorded in both Koumokro and Kouassi-N'Dawa is indicative of ecological conditions conducive to vertical growth for the purpose of light acquisition. In denser stands, competition favours such vertical investment, in contrast to the more open savannah of Pouniakélé, where prolonged dry seasons (November–May) constrain vegetative growth (Silue et al., 2021). A marked variation was observed among the aged arboreal specimens in terms of stem and total height. These disparities underscore the mounting significance of competition for light at advanced stages of development (Chave et al., 2009). With the passage of time, it appears that growth patterns undergo a reversal, with diameter growth stabilising and becoming less influenced by abiotic conditions. The Koumokro and Kouassi-N'Dawa stands, which displayed the most favourable dendrometric and foliar characteristics, share similar ecological conditions and selection pressures that favour slender, vertically oriented individuals. In contrast to these findings, Bokary et al. (2021) reported that crown spread was the main discriminant parameter between agro-ecological zones in Mali, a difference that is likely linked to the finer size class distinctions employed in the present study. With regard to foliar traits, no significant differences in leaf length were observed among the various stands at different developmental stages. However, it was found that petiole length, leaflet width, number of pinnae, and pinnae length consistently distinguished stands, regardless of age. In the Pouniakélé stand, the leaves were distinguished by their narrow and short leaflets, with a high number of pinnae observed at all stages. These results are consistent with those of Teklehaimanot (2004) and Ouinsavi et al. (2010), who demonstrated that populations of *P. biglobosa* in arid regions exhibit increased pinnae numbers as

an adaptive strategy to enhance thermal regulation and resistance to water stress. Such traits are likely to represent an adaptation of the species to arid conditions. In a similar vein, Poljak et al. (2015) demonstrated that leaf variability in trees is strongly influenced by microclimatic factors, thereby confirming that these morphological descriptors contribute to the species' resilience under changing climatic conditions. Across all developmental stages, the presence of morphological variability indicated that tree classification was independent of provenance. Furthermore, an increase in the number of discriminating variables was observed with developmental stage, suggesting that age amplifies morphological differentiation. These findings are consistent with those reported by (Adji et al., 2021), who emphasised the significant impact of ontogeny on the morphology of *P. biglobosa*. In juvenile trees, the disparities between morphological groups were predominantly associated with crown expansion and a limited number of foliar characteristics. Group 3, which comprised exclusively individuals from Koumokro and Pouniakélé, was distinguished by a notably large crown diameter. The absence of Kouassi-N'Dawa trees in this group is likely a consequence of human disturbance, as the expansion of industrial crops in the area has reduced natural regeneration. Local agricultural practices frequently entail the extraction of juvenile trees during the process of land clearance. Conversely, community-based management of *P. biglobosa* in Pouniakélé and Koumokro has been found to promote the preservation of young individuals in fields (Ambe, 2001). This is attributed to the high socio-cultural value of the species in these regions. The notable prevalence of Pouniakélé trees within this group also provides a rationale for the diminutive leaf dimensions observed. This is a prevalent xeromorphic adaptation that serves to mitigate transpiration during the protracted dry season (November–May) (Alonso-Forn et al., 2021). In adult trees, all traits except the number of leaflets distinguished the morphological groups, which included individuals from all three provenances. The first group, which was predominantly composed of trees from Koumokro and Kouassi-N'Dawa, demonstrated superior dendrometric characteristics, indicative of enhanced vigour, a phenomenon that is presumably associated with more favourable environmental conditions, namely superior soil structure, increased water availability, and a bimodal rainfall regime comprising two rainy and two dry seasons. Among the size classes of trees exhibiting advanced age, significant variations were observed across all measured traits. As emphasised by Lauri et al. (2010), age exerts a strong influence on tree morphology. The elevated diversity observed is indicative of the cumulative adaptive capacity of individuals in response to prolonged environmental fluctuations. The analysis revealed that the Koumokro and Kouassi-N'Dawa old trees were predominantly represented in morphological groups 1 and 2. Trees in group 1 exhibited the highest dendrometric characteristics. The foliar traits exhibited by these trees were characterised by the presence of large leaves with a limited number of leaflets and pinnae. This observation serves to substantiate the positive impact of the substantial and frequent rainfall experienced in these two specific localities.

5. Conclusion

Morphological variability in *P. biglobosa* was evident across developmental stages and habitats, with trunk diameter and tree height emerging as key differentiating traits. Leaf characteristics, although less variable among young trees, proved crucial in distinguishing groups and reflected clear age-related

trends. These findings highlight the species' strong phenotypic plasticity and adaptive capacity across environments. Expanding this research to include broader ecological gradients and abiotic factors would further elucidate the mechanisms driving this variability. Overall, the study provides a valuable foundation for the conservation, selection, and sustainable management of this important agroforestry species.

Declarations

Competing Interests

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Author Contribution

Kouassi Ange Carol Koffi: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Léonie-Clémence Kouonon: Writing – review & editing, Supervision, Methodology, validation . Kouamé Guillaume Koffi: Writing – review & editing, Supervision, Methodology, Conceptualization, validation. Lasme Yanne Sylvie Yao: Writing – review & Editing. Raoul Sylvere Sie : Validation, Supervision, Formal analysis.

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Data Availability

The datasets generated and analysed during the current study are not publicly available because there are part of an ongoing PhD thesis and are subject and are subject to intellectual property considerations.

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Figures

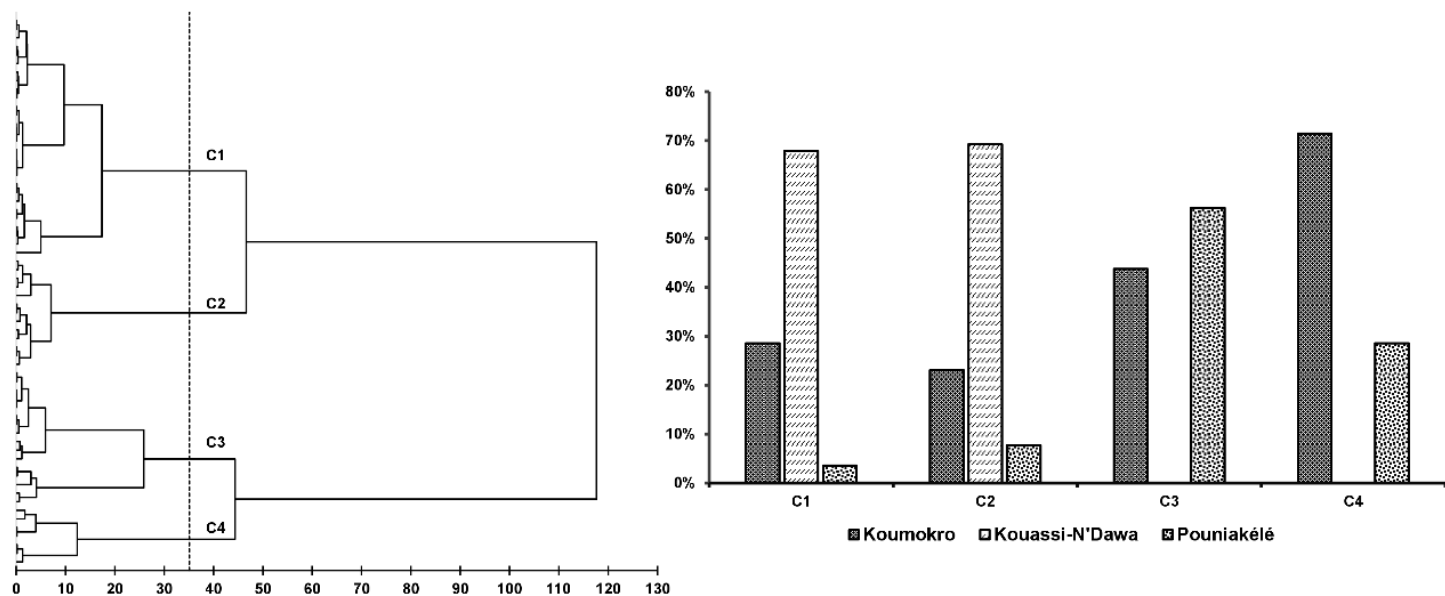


Figure 1

Dendrogram of morphological similarity and distribution of provenances within morphological classes of *Parkia biglobosa* in the young trees

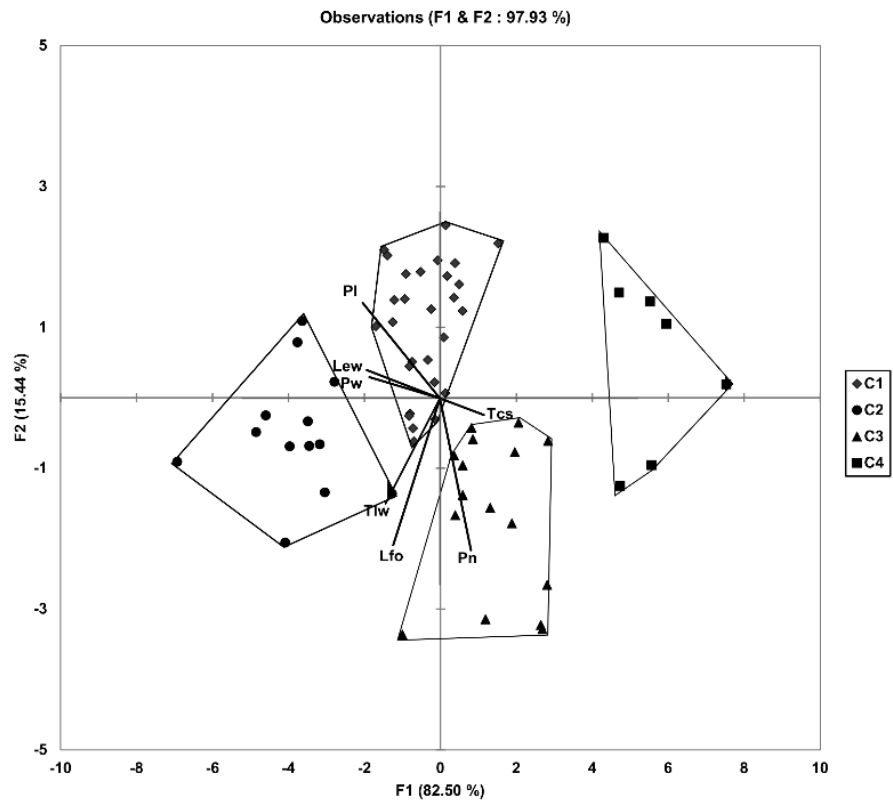


Figure 2

Projection of *P. biglobosa* tree clusters from the young trees size class and descriptors into the factor axis system

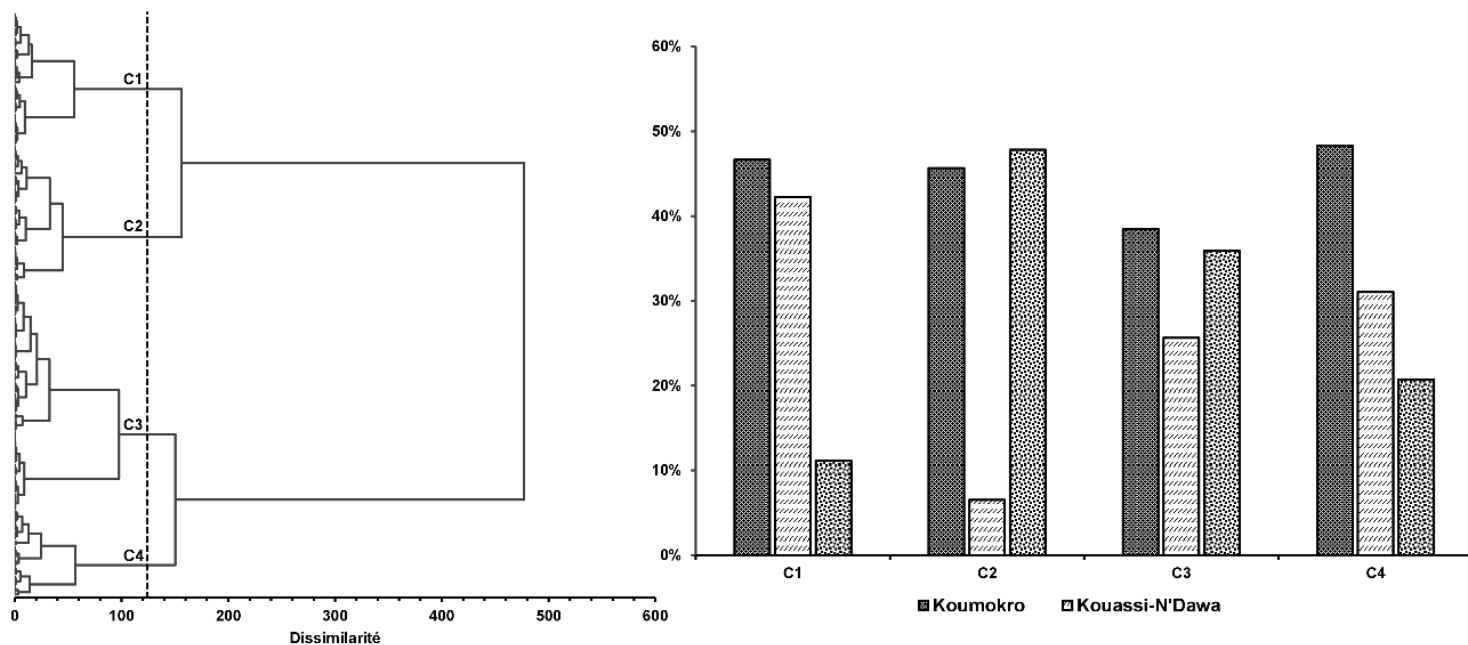


Figure 3

Dendrogram of morphological similarity and distribution of provenances within morphological classes of *Parkia biglobosa* in the adult trees size class

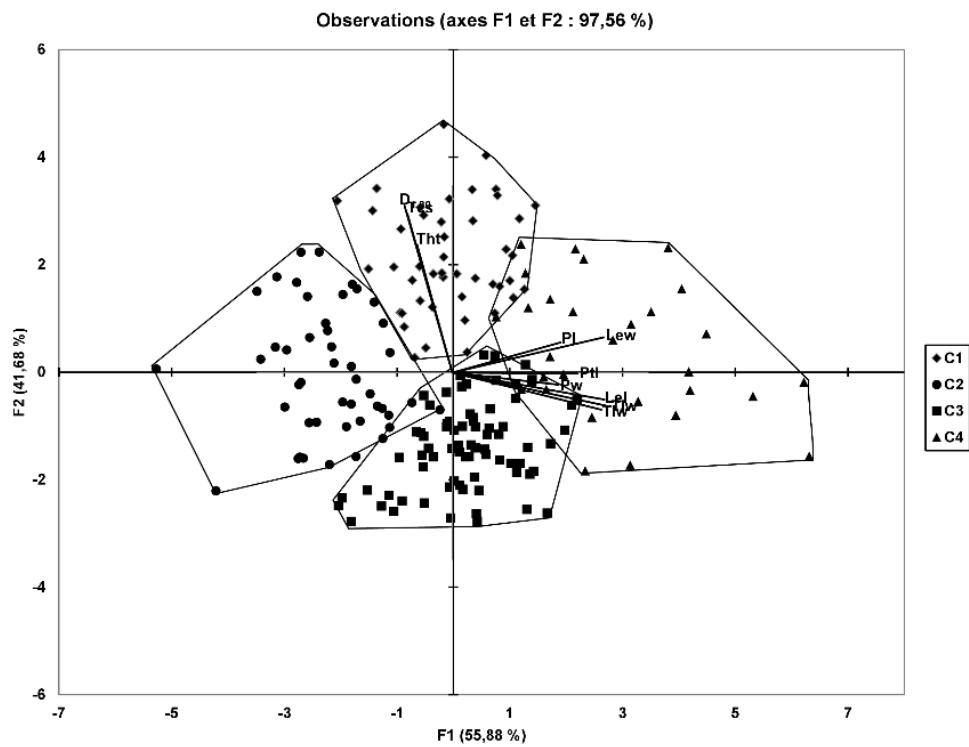


Figure 4

Projection of *P. biglobosa* tree clusters from the adult trees and descriptors into the factor axis system

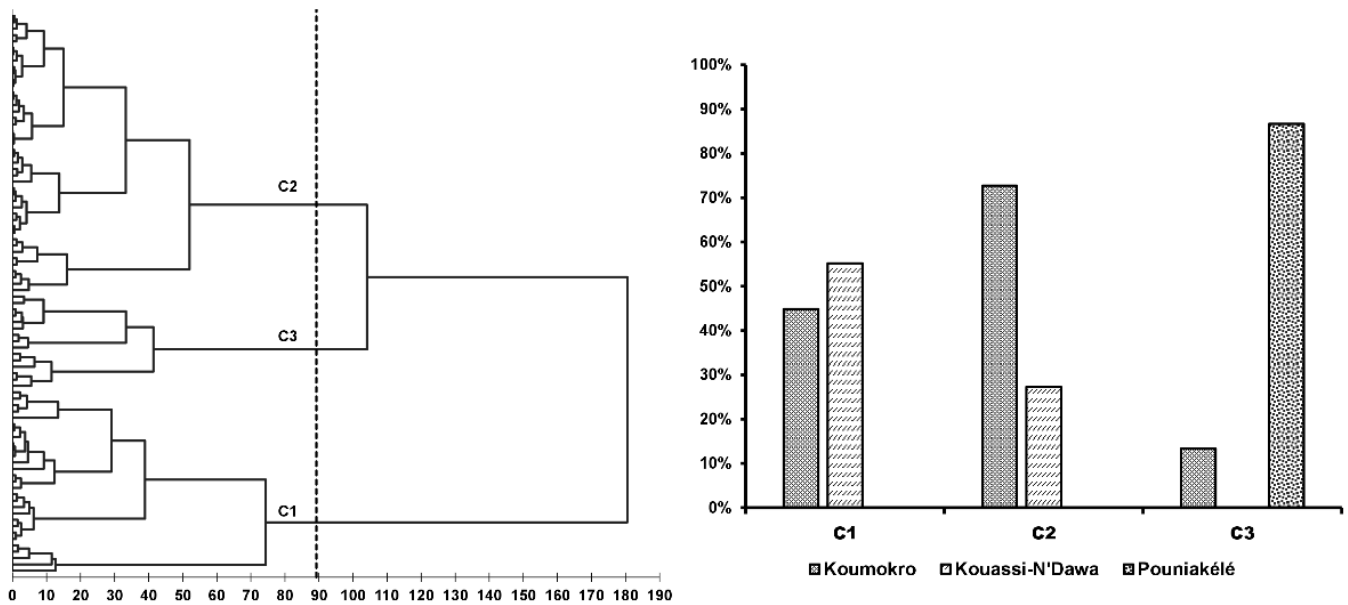


Figure 5

Dendrogram of morphological similarity and distribution of provenances within morphological classes of *Parkia biglobosa* in the old trees

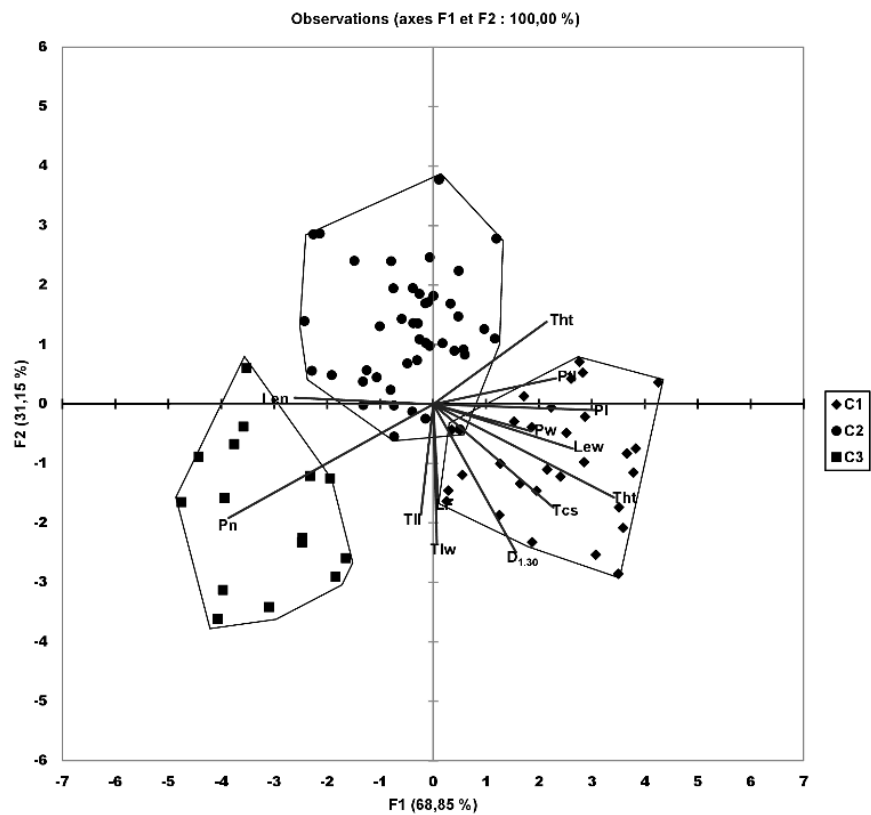


Figure 6

Projection of *P. biglobosa* tree clusters from the young trees and descriptors into the factor axis system