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Research Article

Leaf-based characterization of intermediate forms between Cuban and Honduran mahogany

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Abstract

The genus *Swietenia* includes two mahogany species, *Swietenia macrophylla* (King.), commonly known as Honduran mahogany, and *Swietenia mahagoni* (L.) Jacq, commonly known as Cuban mahogany. There are reports of morphologically intermediate forms between Cuban and Honduran mahogany that have been localized in some Caribbean islands. The main objective of this research is to distinguish morphologically intermediate forms between the parental species *S. mahagoni* and *S. macrophylla* based on leaf morphological characters. Phenotypic data from a total of 357 mahogany trees were collected in the province of Sancti Spiritus, Cuba. Rachis length, petiole length, leaflet length, leaflet width, number of leaflets and number of nerves were evaluated. Morphological descriptor analysis revealed significant differences in the morphometric variables of the evaluated leaves, with rachis length, number of leaflets, leaflet length, petiole length, leaflet width, and number of nerves being significantly higher in *S. macrophylla* than in *S. mahagoni*. ANOVA reflected the variance between all leaf morphological parameters evaluated between the two pure species with statistically significant difference. Using the function obtained in the first DC of the two species, the individuals in the mixed stands were classified into 71 morphologically intermediate forms, 45 *S. macrophylla* and 64 *S. mahagoni*. In the second DC with the two species and the morphologically intermediate forms, Wilks' partial lambda indicates that the variable "leaflet length" with 0.67 contributed most to the overall discrimination.

Keywords: Cuban mahogany; Honduran mahogany; hybrid mahogany; morphometric; *Swietenia*

Introduction

Due to the various global changes that we are experiencing, it is essential to carry out an in-depth analysis and understanding of the variations in the distribution and structure of plant communities, since the proper functioning of ecosystems is closely linked to the specific capacity of each taxon that it integrates to climate

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change, variations in land use, new species compositions and the increase in disturbance factors (Franklin *et al*., 2015).

Climate change and external factors such as intensive agricultural practices, indiscriminate illegal or industrial logging, forest fires and the decline and loss of biodiversity are having a major impact on tropical forests around the world. This affects the capacity of tropical forests to accumulate biomass, the retention and accumulation of carbon, the conservation and sustainability of the biodiversity they contain, and the well-being that forests provide to people (Locatelli *et al*., 2015; Poorter *et al*., 2016; Sun *et al*., 2018; Nytch *et al*., 2023).

Within the order Sapindales is the family Meliaceae, which is a factor of great international importance in the various tropical ecosystems, this family is made up of more than 778 species grouped in 53 genera (Koenen *et al*., 2015). One of these genera is Swietenia, which consists of three species *Swietenia humilis* (Zucc), *Swietenia macrophylla* (King.) and *Swietenia mahagoni* (L.) Jacq.

Cuban or American mahogany, as *S. mahagoni* is known in the countries of this region, is native to South Florida in the USA and several Caribbean islands, particularly the Bahamas, Cuba, Jamaica, the Dominican Republic and Haiti (He *et al*., 2019). In contrast, big-leaf mahogany or Honduran mahogany, as *S. macrophylla* is commonly known, has a natural range from North America to South America, including countries such as Colombia, Brazil, Bolivia, Venezuela, and others (Dünisch *et al*., 2003; Grogan and Barreto, 2005). The third species, *S. humilis*, is found specifically in the Pacific coastal forests of tropical Mexico and Central America (Ovalle-Magallanes *et al*., 2016).

These species are internationally recognized for their unique wood characteristics such as flexibility, mechanical strength, high proportions and aesthetic appeal (Lestari *et al*., 2015; Riana *et al*., 2021). It is therefore used in the manufacture of various high quality products such as musical instruments, handicrafts, wooden flooring, paneling, etc. (Hartigan-O'Connor, 2013). There are several reports of the use of mahogany for medicinal purposes due to the antioxidant, anti-inflammatory and healing properties of its components (Bera *et al*., 2012; Al-Radahe *et al*., 2013; Syame *et al*., 2022). Since 1975 and 1995, the species *S. mahagoni* and *S. humilis* have been listed as endangered due to over-exploitation. In 2003, *S. macrophylla* was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Kim *et al*., 2023). Studies in forested areas of ecosystem systems are limited in most Caribbean Islands (Nelson *et al*., 2020).

There are some reports of morphologically intermediate forms (MIF) between the three species, and some authors report the existence of a putative hybrid between Cuban and Honduran mahogany, found in Cuba, Puerto Rico, the Virgin Islands, Trinidad and Guadeloupe, as well as in Taiwan and Indonesia (Styles, 1981; Maruyama and Ishii, 1999; Lugo and Fu, 2003). The two species naturally form a hybrid that combines desirable characteristics such as the drought tolerance and wood quality of *S. mahagoni* with the fast growth of *S. macrophylla* (Geary *et al*., 1972). Other trials conducted in Caribbean countries such as Haiti and the Virgin Islands have shown greater survival and growth than the parent species (Timyan *et al*., 1997).

There are not many studies focused on the identification of MIF from the morphometric characteristics of the species, due to the excellent characteristics of the hybrid between Cuban and Honduran mahogany, Cuba wants to include this hybrid in the reforestation plans of the country, therefore, it is necessary to identify them primarily from their morphometric characteristics. Therefore, the aim of this study is to identify and discriminate MIF between the parental species *S. mahagoni* and *S. macrophylla* based on leaf morphometric parameters.

Materials and Methods

Study species

The study focused on mahogany, specifically the species *S. mahagoni* and *S. macrophylla*. Cuban mahogany trees are usually large trees, usually exceeding 20 m in height and two (2) m in diameter; when they grow in isolation, they have short and branched trunks, unlike when they develop in competition, the trunks tend to be longer and straighter (Schmidt and Jøker, 2000). In the case of the Honduran mahogany is able to reach 45 m high and two (2) m in diameter, but when it develops under normal conditions only reaches a height of 30 to 35 m and a diameter of 0.8 to 1.6 m (Gillies *et al.*, 1999), the straight and clean trunk of this species can reach 12 to 20 m in length and be slightly grooved with well-developed buttresses up to 2 to 5 m. Some of the characteristics reported in some researches on the putative hybrid between the Antillean and Honduran mahogany species are that in the adult state they are capable of reaching heights of 30 to 40 m and more than 3 m in diameter (Francis, 2003).

The crown of both species is green or dark green, thick, broad and cylindrical hemispherical in shape, the thick branches are well distributed and strong (Bauer and Francis, 1998; Gutiérrez Vázquez *et al.*, 2016). Both *S. mahagoni*, *S. macrophylla* and the putative hybrid between these two species have compound leaves, which are alternate and may be paripinnate or imparipinnate; the composition of the leaflets on the leaf varies from 2 to 6 pairs, which may be ovate or ovate-lanceolate, opposite or subopposite, in both cases dark green. According to Cornelius *et al*. (2004) and Khare (2007), both species have compound leaves, their morphometric characteristics differ from each other; in the case of Cuban mahogany the leaves can reach 10-30 cm in length with leaflets that vary from 2 to 5 pairs, with 2.5-7 cm long and 1.3-3.5 cm wide (Puentes *et al.*, 2002); while in Honduran mahogany the leaves are 25-45 cm long, with three to six pairs of leaflets, rachis without terminal growth (Navarro, 2000), usually opposite, asymmetrical, obovate or lanceolate, 9 to 20 cm long and 6 to 8 cm wide (Sablón, 1984; Bauer and Francis, 1998; Schmidt and Jøker, 2000; Krisnawati *et al.*, 2011; Solórzano López, 2014).

Study site

The study was carried out in the province of Sancti Spiritus (Figure 1), Cuba, with the coordinates (21.9381207, -79.5267729).

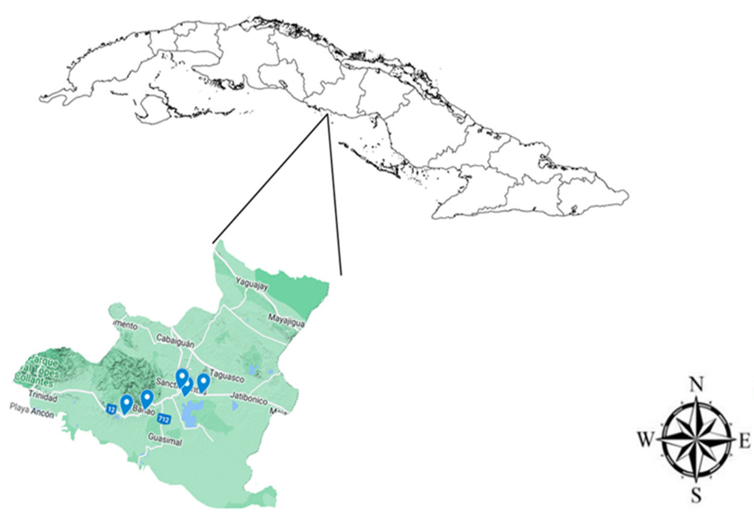


Figure 1. Geographical distribution of the selected populations

Two populations of natural regeneration of *S. mahagoni* were selected for the study (Table 1), which in the past were natural forests of Cuban mahogany, but then were deforested and exploited for agriculture and cattle ranching until 1993 to 1995, both populations are more than 30 years old and the average height of the individuals that make up the population is around 9.94 meters, when these activities stopped and the natural regeneration of the forest began. Due to a collaborative project with the FAO (Food and Agriculture Organization of the United Nations), Honduran mahogany was introduced in Cuba between 1969 and 1970, for the study and possible reforestation work in the country with this species; due to various natural phenomena and urbanization, the presence of these first seedlings is practically null, for this a remnant of one of the first plantations of Honduran mahogany in Cuba was selected between 1969 and 1970, this remnant is approximately 55 years old and the average total height of the individuals that comprise it is around 16.47 meters high; two mixed stands were also selected where there is the presence of both species and MIF, established between 1982 and 1984, the average age of these mixed stands is around 42 years old and the average total height of the individuals that make up the stand is 15.74 meters. The total area covered by this study was more than 6 ha. This is representative since, according to the country's forest management and exploitation plans, the establishment of the different forest niches is between 1 and 2 ha. Sampling of all individuals was conducted from March to early May 2023, before the onset of spring in Cuba.

Table 1. Selected individuals by population

Pop.	SP.	n	Lat.	Long.	Alt.	Temp.	HR	PP
La Güira	*S. mahagoni*	80	21.78942	-79.64634	60	25.1	78	120.1
Modelo	*S. mahagoni*	80	21.89687	-79.41949	5	24.6	80	127.75
Colón	*S. macrophylla*	17	21.91925	-79.44355	15	24.5	79	127.75
Banao	Both species and MIF	90	21.82337	-79.56849	30	23.6	86	130.3
Emigdio	Both species and MIF	90	21.91972	-79.35641	35	24.3	82	122.5

Population name (Pop.), Predominant species (Sp.), Total number of selected individuals (n), Latitude (Lat.), Longitude (Long.), Altitude (Alt.) in meters, Average monthly temperature in degrees Celsius (Temp.), Monthly mean relative humidity in percent (HR) and Monthly average precipitation in millimeters (PP)

For each individual, 3 leaves were selected (Gillies *et al*., 1999; Curtu *et al*., 2007; Enescu *et al*., 2013; Bündchen *et al*., 2015; Apostol *et al*., 2017; Des *et al*., 2020; Olvera Moreno *et al*., 2022) from the eastern side of the tree, to avoid possible errors in the parameters evaluated based on the development morphological and photosynthetic capacity of the leaf. Since these species have compound leaves with more than 4 to 5 pairs of leaflets per compound leaf, this number of selections was considered representative and sufficient, and a total of 771 leaves were sampled. To collect the leaves for the study, the canopy was divided into three parts: high, medium and low, where the adult leaves and branches were selected to avoid errors, since the young leaves and branches, which have not completed their development, can influence the errors. Measurements were made on fresh leaves after collection. In turn, each tree was marked with paint and its coordinates were taken. In addition, historical provincial meteorological data for the years 1991 to 2022 were requested from the Provincial Metrological Center of Sancti Spíritus, Cuba (Table 1).

Morphological analysis

In the leaves selected for each individual, the parameters rachis length (RL), number of leaflets (NL), petiole length (PL), leaflet length (LL), leaflet width (WL) and number of nerves (NN) were measured using a graduated ruler (mm) (Figure 2). According to the morphologic characteristics described in various literatures (Bisse, 1981; Albert Fuentes and Zavaro Pérez, 1995; Francis, 2000; Sánchez and Trapero-Quintana, 2018; Montiel *et al*., 2020; Cocuzza *et al*., 2021), based on the leaf morphometric variables observed and analyzed for each individual in the different populations, the Analysis of Morphological Descriptors (MED) was performed using IBMSPSS Statistics v20.0 (2011) software. The t-test was performed to test the significance level of the means obtained in the leaf variables of the species evaluated in the study. For homogeneity of variances, Levene's test was performed and when the variance of the groups was unequal, Welch's t-test was performed. STATISTICA v8.0 software was used for statistical analysis of the data (StatSoft, 2008), to determine the variance of the parameters between the species *S. mahagoni* and *S. macrophylla*, an Analysis of Variance (ANOVA) was performed; in turn, discriminant functions were constructed from the Discriminant Function Analysis (DC) in order to discriminate between the two species of mahogany and the putative hybrid based on the morphometric variables of the leaves selected for this study, in order to analyze the level of interrelation between the populations based on the variables with the highest discriminant power, a Cluster Analysis (CA) was performed.

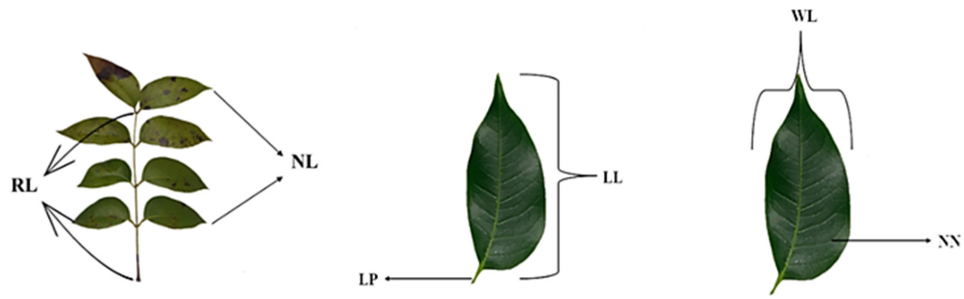


Figure 2. Graphical representation of the evaluated indicators

Results

Morphological descriptors analysis

The morphological differences between the species *S. mahagoni* and *S. macrophylla* (Table 2) showed statistically significant differences (p≤0.05) in the 6 variables evaluated. The length of the rachis is longer in *S. macrophylla*, being 79% longer than in *S. mahagoni*. As for the number of leaflets, due to the difference between the morphometric dimensions of the compound leaves between the two species, they are distributed in smaller quantities in Cuban mahogany and in greater proportions in Honduran mahogany with a difference of 39.49% with respect to the other species. In the rest of the morphological characteristics of the leaflets such as petiole length, leaflet length, leaflet width and the number of nerves in the species of *S. macrophylla* are identified by having higher mean values with 35.29% (LP), 70.99% (LL) and 65.65% (WL) with respect to *S. mahagoni*. Regarding the number of nerves present in each leaflet of the compound leaves, Cuban mahogany is surpassed in the number of nerves by 39.27% compared to those present in Honduran mahogany.

Table 2. Coefficients of variation, mean values for the 6 leaf traits of the two species and significance of their differences

Leaf des.	*S. mahagoni*					*S. macrophylla*					t -value (t & Welch t-test)	p-Value
	Min	Mean	Max	SD	CV%	Min	Mean	Max	SD	CV%		
RL	2.93	9.21	16.43	±2.28	24.76	19.23	43.60	72.60	±14.21	32.59	99.25	**.00+**
NL	4.00	6.68	11.33	±1.25	18.71	8.00	11.04	15.67	±1.87	16.94	89.23	**.00+**
LP	0.23	0.44	0.69	±0.08	17.78	0.49	0.68	0.93	±0.14	20.59	42.19	**.00+**
LL	3.13	4.56	7.53	±0.76	16.67	10.68	15.72	20.90	±2.72	17.30	284.10	**.00+**
WL	1.43	2.15	4.10	±0.45	20.93	4.92	6.26	8.36	±0.99	15.82	281.32	**.00+**
NN	10.57	14.23	21.19	±1.92	13.42	19.42	23.47	26.87	±2.28	9.71	260.59	**.00+**

Statistically significant p-value (p≤0.05) of the morphological leaf descriptors [rachis length (RL), number of leaflets (NL), petiole length (PL), leaflet length (LL), leaflet width (WL) and number of nerves (NN)] among the two species (*S. mahagoni* and *S. macrophylla*) are given in bold; p-values calculated using Welch t-test are indicated with "+" symbol.

ANOVA

When evaluating the different morphometric indicators of the selected leaves in *Swietenia mahagoni* and *Swietenia macrophylla* species, it can be observed in Figure 3 that there are significant statistical differences ($p \leq 0.05$) between the two species. The difference between the values of *S. mahagoni* and *S. macrophylla* in the different treatments was RL with 34.39, NL with 4.84, PL with 0.21, LL with 11.16, LW with 4.11 and NN with 9.17 cm, which represents a difference of 78.88, 43.85, 31.05, 71.01, 65.66 and 39.08 % between the two species.

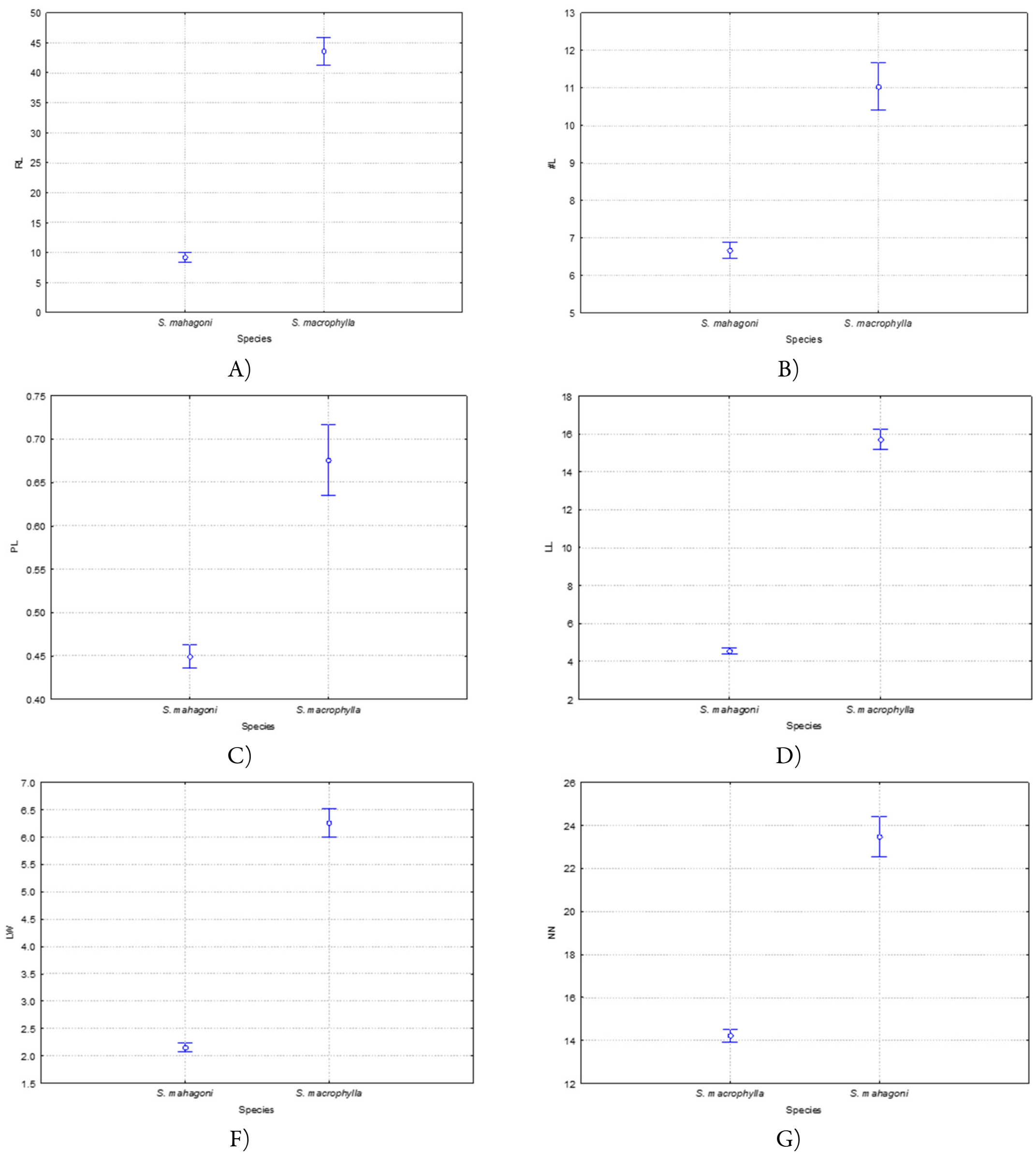
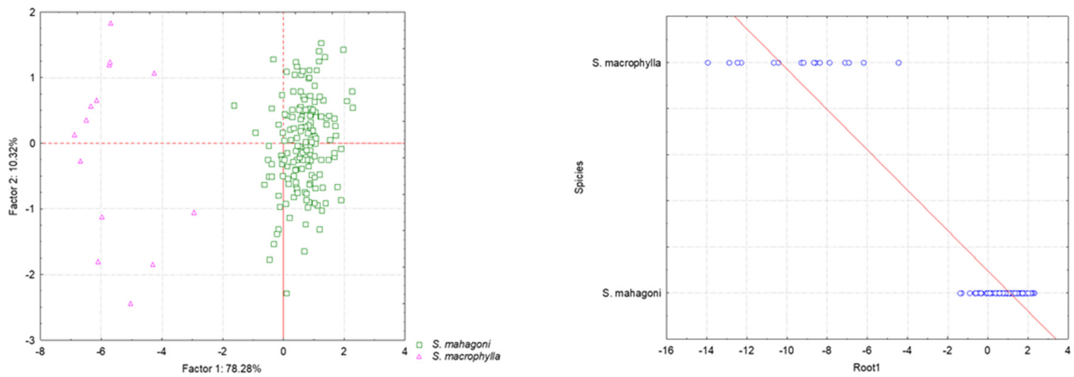


Figure 3. Analysis of variance of the indicators A) Rachis length (RL), B) Number of leaflets (NL), C) Petiole length (PL), D) Leaflet length (LL), E) Leaflet width (LW), F) Number of nerves (NN) with ($p \leq 0.05$)

Discriminant analysis and Principal Component Analysis

In Figure 4 A the PCA analysis was carried out only with the data collected in the populations of the two species *S. mahaoni* and *S. macrophylla*, Factor 1 explains 78.28% of the variation of the variables and is represented by the length of the leaflet and the length of the rachis; while Factor 2 explains 10.32% of the variation and is associated with the length of the petiole. Figure 4 B shows the discriminant analysis only for the two species, where the variable "leaflet length" was the one that presented the highest discriminant power for $p<0.05$, with a partial Wilks' lambda value of 0.85. The equation that allows discriminating between these two species was elaborated as Root 1: 581.9 - 79.39*LL; from the graphic representation of this analysis, it is considered that the MIF will be located within the range of (-1.4; -4), for which the Root 1 obtained was used to establish the classification within the mixed stands.



A) B)

Figure 4. A) Principal Component Analysis and B) Discriminant analysis only with the two pure species *S. mahagoni* and *S. macrophylla*

By using the discriminant function obtained previously in the mixed plantations, it was possible to classify the individuals belonging to them. The classification obtained in the mixed stand of Emigdio (Figure 5 A) of a total of 90 individuals 56 belonging to *S. mahagoni*, 2 individuals belonging to *S. macrophylla* and 32 MIF; while in B) belonging to the mixed stand of Banao of the 90 individuals, 8 belonged to *S. mahagoni*, 46 to *S. macrophylla* and 39 MIF.

A) B)

Figure 5. Classification of the individuals of each mixed stands A) Emigdio and B) Banao

Having the classification of each species and the MIF from the first discriminant analysis, we proceeded to perform a new PCA with the two species and the MIF (Figure 6 A); where Factor 1 explains 69.56% of the variation of the variables and is mainly represented by rachis length and leaflet length, while Factor 2 explains 15.69% of the variation of the data and is more associated with petiole length. A new DA was performed with the morphological parameters collected with the species *S. mahagoni*, *S. macrophylla* and the MIF identified previously. The highest Wilks lambda values (0.14-0.21) were found in 4 of the 6 parameters analyzed, which were leaflet length, number of nerves, leaflet width and petiole length. The partial Wilks' lambda indicates that the variable "leaflet length", with a value of 0.67, had the highest contribution to the overall discrimination, since according to Fisher (1936), the lower the value of partial Wilks' lambda, the greater the discriminatory power. The following two discriminant functions were obtained, Root1: 375.62-69.95*LL+8.32*#N-13.25*LW+146.46*PL and Root2: 337.68+82.54*LL-21.10*#N-164.18*LW-48.51*PL.

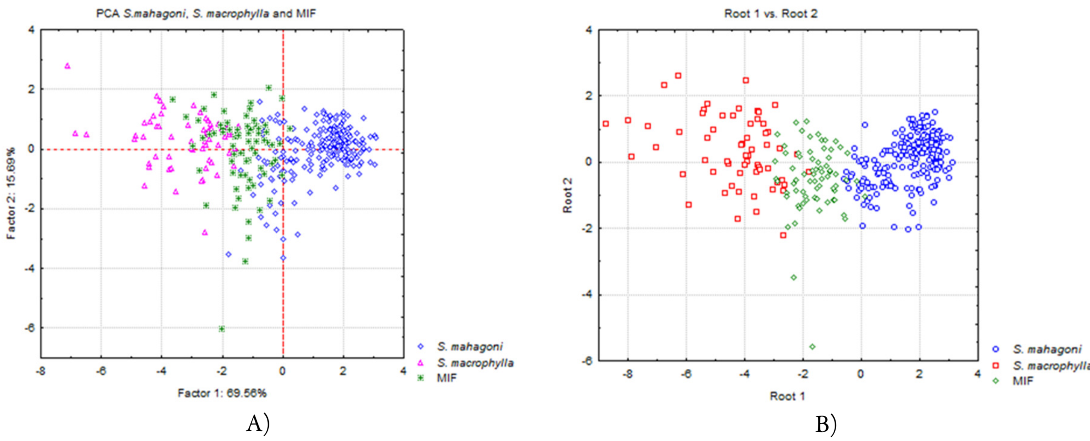


Figure 6. A) PCA and B) DA with the two species and the MIF

Root 1 provides the most significant discrimination for the species of *S. mahagoni* among the others, this discriminant function represents 98.61% of the variance. This function is marked by negative coefficients for leaflet width and leaflet length and positive values for number of veins and petiole length. Root 2 allows distinguishing between the MIF which have negative values for this function and the two species which have positive values. Figure 6B shows how the individuals are graphically distributed from the discriminant functions obtained, where the species *S. mahagoni* which presents positive values in Root 1 and Root 2 according to the means of the canonical variables (MCV), in the case of the species *S. macrophylla* presents negative values in Root 1 and positive values in Root 2 and the MIF present negative values in both discriminant functions based on the morphological characteristics of the leaves.

During the first field sampling, the number of individuals sampled was 160 belonging to the species *S. mahagoni* in two populations of natural regeneration, 180 individuals belonging to two mixed stands and 17 individuals of the remnant of the species *S. macrophylla*. After performing the discriminant analysis based on the main morphological characteristics of the leaves, the classification matrix predicted the classification of the individuals with a success rate of 94.96% based on the four variables with the highest discriminant power (Table 3), leaving 220 individuals belonging to Cuban mahogany, 54 to Honduran mahogany and 83 MIF in total. The percentage of misclassification in each of the species and MIF was 2.68% in *S. mahagoni*, 14.52% in *S. macrophylla* and 4.23% in the MIF.

Table 3. Prediction matrix based on the main morphological characteristics of the leaves of individuals evaluated

Group	Percent Correct	*S. mahagoni* p=.62745	*S. macrophylla* p=.17367	MIF p=.19888
S. mahagoni	97.32	218	0	6
S. macrophylla	85.48	0	53	9
MIF	95.77	2	1	68
Total	94.96	220	54	83

The first column represents the percentage of cases that have been correctly classified in each group by the current classification functions. The next columns show the number of cases that are misclassified in each group, and how they are misclassified.

Cluster analysis

The populations of the two species and the mixed plantations were grouped into a primary cluster (Figure 6). In the primary clusters we can appreciate how the two species of Antillean mahogany and Honduran mahogany are separated; showing a level of discrimination between the populations of these species and the mixed stands in relation to the 5 of the 6 morphological characters evaluated with discriminating power (RL, LP, LL, WL and NN) in which they present statistically significant differences for $p \leq 0.05$; resulting in the separation of the populations of the two species of mahogany and the mixed plantations.

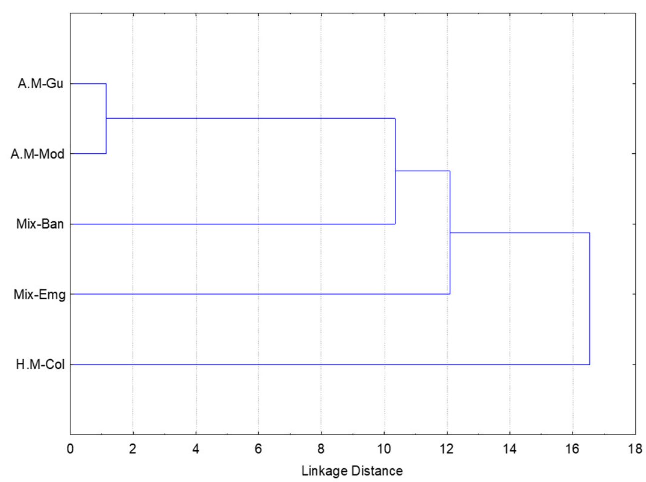


Figure 6. Cluster analysis using the variables RL, LP, LL, WL and NN
In this figure, A.M stands for *S. mahagoni*, H.M stands for *S. macrophylla*, Mix stands for mixed stands and the other three letters are the abbreviation of the populations as in Table 1

Discussion

Morphological descriptors analysis

Leaf morphological characteristics play an important role in taxonomic classification and species identification. Variability in leaf dimensions between populations or individuals can contribute to the delineation of distinct species or subspecies (Platt, 1901; Francis, 2003; Khare, 2007; Grogan *et al*., 2011). Leaf dimensions, such as length, width, and shape, may reflect adaptations to local environmental conditions (Gullison *et al*., 1996; Brown *et al*., 2003; Lugo and Lowe, 2012; Pancel, 2016). Leaves are the most sensitive organ to temperature changes, therefore leaf morphological and physiological traits are closely related to cold stress acclimation and subsequently affect tree survival and growth (Betancourt, 1976; Bisse, 1981; Rodan *et al*., 1992; Jennings *et al*., 2001; Basil, 2007).

Our research clearly showed that there were significant differences between the two mahogany species, Cuban and Honduran, in the parameters selected for evaluation in this study. The species *S. macrophylla* presented the highest values in all the different leaf morphological parameters evaluated. In a study by Palacios *et al*. (2023) carried out an analysis of morphological descriptors in the species *Cedrela angusticarpa* that belongs to the Meliaceae family like mahogany, where they arrived at the conclusion that *C. angusticarpa* is related to *C. odorata*; among the main morphological characteristics that distinguish these two species is the shape of the leaflets that vary from oblong-lanceolate to oblong-falcate, the shape and dimensions of the inflorescence in the form of a panicle that in the species *C. angusticarpa* has a curved shape with 15-40 cm in length while in *C. odorata* the fruits stand out with a robust-erect shape with dimensions of 40-70 cm in length. odorata has a curved shape with 15-40 cm in length while in *C. angusticarpa* it has a robust-erect shape with dimensions of 40-70 cm long and, in this last species the fruits stand out for having obovoid characteristics with an acute base while in the other species the fruits are oblong-ellipsoid with a rounded or obtuse base.

On the other hand Akinyele et al. (2020) carried out a morphological comparison of the leaf epidermis in the species *Azadiracta indica*, *Cederella odorata*, *Khaya sensegalensis* and *Khaya grandifoliola* belonging to the family Meliaceae. These authors reported that the best taxonomic descriptors in these four species are the epidermal layer, cuticle thickness, epidermal layer thickness, mesophyll organization, xylem shape, presence or absence of trichome and trichome type, which enable the correct identification and limitation between these four different species.

Sarma *et al*. (1992) investigated leaf morphological characteristics related to the taxonomy of 11 species of the family Meliaceae (*S. mahagoni*, *S. macrophylla*, *Aglaia roxburghiana*, *Azadirachta indica*, *Cedrela serrata*, *Cedrela toona*, *Cipadessa baccifera*, *Heynea trijuga*, *Melia azedarach* and *Somyda febrifuga*). These authors reported that the primary leaf vein in *S. mahagoni*, *A. indica* and *A. roxburghiana* species is mostly straight but curved, while in *C. baccifera* and *H. trijuga* species it is slightly curved, another characteristic that stands out is how the terminations of the veins vary where they include traditional tracheids (in all species except Honduran mahogany), as well as the presence of tracheids in all species; the authors state that the presence of the bundle sheath constitutes a good diagnostic character because of the 11 species investigated of the Meliaceae family it is present only in three species, in *Cedrela* where it is part of all grades of veins, in the species *A. indica* and *S. mahagoni* where it is located only in the primary and secondary veins.

Variability in leaf dimensions within populations can indicate responses to resource availability, such as light, water, and nutrients. Trees growing in resource-rich environments may exhibit larger leaves, while those in resource-limited conditions may have smaller leaves. Leaf morphology can also be used to identify potential hybrids between different mahogany species. Hybrid individuals may exhibit intermediate leaf characteristics compared to their parent species, reflecting genetic introgression and hybridization events (Lamb, 1960; Whitmore and Hinojosa, 1977; Fetcher *et al*., 2003; Lemes *et al*., 2003; Daquinta *et al*., 2007; Oliveira, 2018; Meza Picado *et al*., 2020).

Additionally Liu *et al*. (2018) when carrying out a geometric morphometric analysis of the leaf shapes of *Quercus dentata* and *Quercus aliena* they reported significant leaf morphometric differences between these two species where *Q. aliena* had a longer petiole, a wider basal region and a narrower leaf blade tip than *Q. dentata*.

In turn Apostol *et al*. (2017) observed variability in leaf morphology in the southern Carpathian region of Romania in pedunculate oak and gray oak species. The analysis of morphological descriptors reported statistically significant differences between the two species in 12 of the 15 variables evaluated, these being pubescence intensity (PU), leaf abaxial color (CL), basal lamina shape (BS), lamina length (LL), lamina length (LL) and lamina length (LL), lamina length (LL), petiole length (PL), lobe width (LW), sinus width (SW), lamina length at widest width (WP), lamina shape (LS), petiole ratio (PR), lobe depth ratio (LDR) and lobe width ratio (LWR). In turn, they reported how leaf dimensional traits vary between *Quercus pedunculiflora* (*Q. pedunculiflora*) and *Quercus robur*, where leaf dimensions of the latter are characterized by higher mean values with 5.4% (LL), 30.5% (PL) and 8.0% (LW) than those present in *Q. pedincuflora*.

Furthermore Bündchen *et al*. (2015) investigated in a subtropical forest in southern Brazil the leaf structure of woody species in the canopy and understory, where they reported that *Cedrela fissilis*, *Cupania vernalis*, *Matayba elaeagnoides* and *Nectandra lanceolata* had lower specific leaf area, but higher density of stomata and thickness of palisade parenchyma. While the rest of the evaluated species, *Allophylus guaraniticus*, *Lantana brasiliensis* and *Gymnanthes concolor*, presented a greater thickness of the spongy parenchyma and relative percentage of intercellular spaces in the spongy parenchyma.

ANOVA

These results partially coincide with those reported by Li *et al*. (2021) who investigated the genetic, geographical and climatic factors influencing leaf morphological characteristics of *Quercus aquifolioides* Rehder & E.H. Wilson, and reported how the leaf size parameter expressed the highest total variance with 47.4% and 40% associated with inter-tree and leaf effects.

On the other hand, the results obtained in the analysis of variance are in partial agreement with those obtained by Fortini *et al*. (2015), who, using one-way ANOVA and the Kruskal-Wallis test, reported discriminating traits between the species of *Q. frainetto*, *Q. petraea* and *Q. pubescens* in the foliar parameters. The leaf traits lobe width and petiole ratio allowed the differentiation between *Q. frainetto* and the other two species that showed similarities between them; while in the parameter's compactness and lobe width ratio *Q. frainetto* showed higher correlation with the species *Q. pubescens*.

Possibly the differences that these two mahogany species have in the morphometric characteristics of their leaves are not only due to the genetic structure of each species, but also to the natural range in which they are distributed and the edaphoclimatic conditions in which they develop. Antillean mahogany is found naturally in most of the Caribbean islands and the southern part of Florida in the United States of America, where average temperatures range between 25 and 26 °C, where flat areas are abundant and its distribution tends to decrease as altitude increases (Platt, 1901; Francis, 2003; He *et al*., 2019),while the natural distribution range of Honduran mahogany goes from Mexico to the Amazon rainforest where the predominant climate is equatorial with rainfall varying between 1500-500 mm per year, the optimum temperature for its development ranges between 23 and 28 °C, it is able to be located up to 1000 m above sea level (Cheng-Jun *et al*., 2003; Dünisch *et al*., 2003; Pancel, 2016).

In turn, Gerber and Les (1994) investigated leaf morphometric characteristics in different geographical locations and habitats among different species of Myriophyllum (Haloragaceae); ANOVA showed that species distributed in the sptentorial habitat showed statistically lower values ($P < 0.05$) for the indicators leaf mass, volume and surface area than species in the generalized unit. At the same time, they reported the highest variances in the parameters surface area, volume, dry mass and surface volume ratio among the species located in the different geographical units. Meanwhile, Pérez-Pedraza *et al*. (2021) reported statistically significant variance among all selected parameters except for the variables leaf apex angle and leaf base in *Q. acutifolia* and *Q. grahamii* species.

Discriminant analysis and principal component analysis

Seo *et al*. (2021) by means of discriminant analysis were able to classify and identify 27 vegetative characters of the *Salix caprea* and *Salix gracilistyla* species, and the hybrid between these two species. The characters with the highest discriminating power between the two species and the *S. caprea* x *S. gracilistyla* hybrid were the type of lower leaf hair, type of lateral vein, number of striae per stipules, twig color, length of winter bud, and type of winter bud hair.

On the other hand, the results obtained partially coincide with those reported by Curtu *et al*. (2007) who investigated the levels of hybridization and introgression in populations of *Quercus* spp. When performing the discriminant analysis, these authors were able to explain 67.5 and 30.4 % of the variations present in the different oak species present in the two functions obtained; the most important characters in the differentiation between species were the proportion of the petiole and the basal shape of the lamina. Of the species present, only the species *Quercus petrea* and *Quercus pubescens* could not be differentiated using only the morphometric parameters of the leaves.

Yang *et al*. (2022) by analyzing variations in leaf morphology in the species *Q. dentata* in three different locations in Hebei and Heban provinces. The fundamental characters to distinguish the origin of the samples were circularity, leaf width and width-length ratio; with the discriminant analysis these authors were able to classify the samples according to their origin with 74, 68 and 74% of precession.

On the other hand, a study focused on the main morphometric characters of leaves and fruits that discriminated between two oak species (*Q. virgiliana* and *Q. pubescens*) was developed by Enescu *et al*. (2013), the most important discriminating factor among the 918 individuals selected for the research from more than 20 stands in different locations in Romania was the length of the dome, where only 42 individuals showed a dome peduncle greater than 1.5 cm, while 623 individuals, representing more than 80 %, had the same parameter with a value of less than 0.8 cm and the rest of the individuals had an intermediate morphology ranging between 0.8 and 1.5 cm.

By means of discriminant analysis of leaf morphological parameters, the following parameters were used Akli *et al*. (2022) were able to discriminate between four oak species and hybrids (*Q. afares*, *Q. suber*, *Q. canariensis* and *Q. ilex*), where the discriminant equations obtained explained 93.05% of the total variation among individuals. On the other hand Curtu *et al*. (2011) analyzed 844 individuals in seven populations of *Q. robur* and seven populations of *Q. pedunculiflora* and a mixed forest where both taxa were located. The leaf parameter abaxial lamellar pubescence showed the highest discriminant power between the two oak species followed by the petiole length character. With the discriminant function obtained, the authors were able to classify the individuals located in the mixed forest of the Danube Delta into 47 individuals of the species *Q. robur* and 52 individuals corresponding to *Q. pedunculiflora*.

Cluster analysis

These results are partially in agreement with those obtained by Wang *et al*. (2020) who, based on cluster analysis, divided the 13 sampled populations into three groups when evaluating the morphological variation of *Cynodon dactylon* species and its relationship with the environment. The main characteristics that presented sources of diversity from the principal component analysis in the morphological variables evaluated in the study populations were the length of the erect shoot leaf, the width of the erect shoot leaf, and the lengths of the erect shoot internodes and the stolon, as determined by the principal component analysis carried out by these authors.

In turn, in a study on the silvicultural performance of five forest species (*Dipteryx odorata*, *Parkia decussata*, *Jacaranda copaia*, *Acacia mangium* and *Swietenia macrophylla*) in the Amazon rainforest in Brazil conducted by Machado *et al*. (2018) the hierarchical cluster analysis showed that the species *D. odorata* and *P. decusata* showed similarities forming a group with a slightly lower similarity with *J. copaia*, these three species reported the greatest similarities in the diametric variables evaluated diameter at breast height, total height, crown projection area and volume of the commercial cylinder in this study. On the other hand, *D. odorata*, *J. copaia* and *P. decussata* showed less similarity with the other native species *S. macrophylla*.

In turn Romero *et al*. (2000) when studying from the phenotypic point of view the taxonomic delimitation of the species *Quercus acutifolia* and *Quercus conspersa*, they obtained two large groupings in the phenogram obtained through the cluster analysis, in which one of the groupings were located the typical representatives of *Q. acutifolia*, located in the upper part of the phenogram and including 23 populations of the 42 selected in this study; while the second group was composed of the rest of the 19 populations which occupied the lower part of the phenogram and belonged to the species *Q. conspersa*.

Hierarchical clustering analysis was performed to obtain how the populations are graphically grouped according to the foliar parameters selected for analysis (Yildirim and Turna, 2021). On another hand, Navarro-Cerrillo *et al.* (2018) in the hierarchical grouping of the mean data of *Quercus ilex* populations, the eastern ecotypes selected for the study were clearly delimited from the four westernmost ecotypes. The authors evaluated the growth and physiological responses of 11 ecotypes of *Q. ilex* under identical environmental conditions.

Also González-Rodríguez and Oyama (2005) in evaluating how leaf morphometric characteristics varied in *Quercus affinis* and *Quercus laurina* species in Mexico, reported how cluster analysis structured two main groups of populations, reporting phenotypic variation in the analyzed species. All leaf traits evaluated (total length, petiole length, maximum width, number of leaf margin teeth, lamina length and distance from the leaf base to the point of maximum width) showed significant statistical differences between populations.

Conclusions

Using the foliar morphological variables through morphological descriptors analysis and analysis of variance between the species *S. mahagoni* and *S. macrophylla*, it was possible to observe that there is a significant variance between the parameters evaluated between each species, which allows the identification of these from the foliar characters evaluated. On the other hand, after performing the discriminant analysis and a principal component analysis first with the two pure species to observe the distribution and the discriminant power between the two species and with the obtained discriminant function was possible to classify each individual of the mixed stands, obtaining 71 MIF in first instance. A second discriminant analysis was then carried out with the three classifications *S. mahagoni*, *S. macrophylla* and the MIF, it was obtained that the parameter leaflets length was the parameter with the highest discriminant power. After the second discriminant analysis, each individual was classified by means of the classification matrix based on the main parameters with the highest discriminant power 220 *S. mahagoni*, 54 *S. macrophylla* and 83 MIF were identified, with a percentage of correct classification of 94.96%. The cluster analysis reflected how the populations assessed were distributed in a primary cluster, where both species and mixed stands were separated by the discriminant power of the variables used. At the same time, the morphological characteristics evaluated showed that there is a great deal of variation among individuals belonging to the Honduran mahogany. Future studies would address from a genetic point of view if the results obtained in this research from the morphometric data of the leaves coincide or vary.

Authors' Contributions

Conceptualization: LC and EC; Data curation: LC, EC and CC; Investigation: LIRC, AGTB, JFLE and LADF; Methodology: LC and EC; Supervision: LC; Writing - original draft: LIRC, LC and EC; Writing - review and editing: LIRC.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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