Bulletin of the *Transilvania* University of Brasov
Series II: Forestry • Wood Industry • Agricultural Food Engineering • Vol. 18(67) No. 2 – 2025
https://doi.org/10.31926/but.fwiafe.2025.18.67.2.4

FROM ABANDONED LANDS TO GENETICALLY ROBUST STANDS: NUCLEAR GENETIC DIVERSITY AND FINE SCALE SPATIAL GENETIC STRUCTURES IN CUBAN MAHOGANY (*Swietenia mahagoni)*

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Abstract: *The conservation of genetic diversity is critical in fragile biomes such as tropical ones, where fragmentation and habitat loss are particularly intense. Intensive exploitation of Swietenia mahagoni (Cuban mahogany) has led to severe fragmentation and a significant reduction in the natural habitat of this species. There are no genetic studies on S. mahagoni in Cuba, which limits the design of robust conservation strategies. In this context, the present study aimed to evaluate the nuclear genetic diversity and the spatial genetic structures (SGSs) of two naturally established Cuban populations of S. mahagoni, analysing 160 individuals with eight nuclear SSRs previously validated in other Swietenia species. SSR nuclear markers revealed high genetic diversity and mostly intra-population variation. AMOVA showed that most of the genetic variation is within populations, with low but significant differentiation between populations. At a fine scale, autocorrelation correlograms showed no significant spatial genetic structure, which suggests that the processes that operated after establishment were determined by multiple seed sources and effective gene flow, diluting detectable family aggregation. Sp values (0.0110-0.0111) were very small for both stands. Taken together, these results provide a genetic basis for the conservation and sustainable management of Cuban mahogany.*

Key words: *Swietenia mahagoni, genetic diversity, conservation, microsatellites, Cuban tree species.*

1. Introduction

Genetic diversity in forest tree populations forms the basis for the adaptive capacity of stands in the face of environmental changes [31]. In

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populations that have established naturally following the abandonment of anthropogenic uses (agriculture, grazing or forestry), this heritable variation reflects both colonisation processes and the demographic traces of the past. Foundational bottlenecks, the composition of seed sources, the magnitude of gene flow with remnants, and the resulting spatial structure can generate patterns of allelic richness and population differentiation that differ markedly from primary forests, with direct implications for ecological resilience and in situ conservation [20, 40].

Spatial genetic structure (*SGS*) provides indirect information on gene dispersion and local demographic processes in tree populations and is therefore relevant for management under scenarios of disturbance, habitat degradation, and environmental change [3, 22]. In general, *SGS* is mainly determined by limitations on dispersal, local recruitment, and non-random mating, which tend to group related individuals at short distances [23]. In this context, anthropogenic disturbances can intensify *SGS* by modifying reproductive structure, mating neighbourhoods and effective dispersal; in some cases, stands with lower individual density may show more pronounced *SGS* due to changes in these processes [3].

In continuous populations, *SGS* can arise both through differential selection at microenvironmental scales and through restricted gene flow due to limited pollen and seed dispersal [14]. Classical studies have characterised genetic divergence between populations using neutral molecular markers and measures of genetic distance, while spatial autocorrelation analyses have been widely used to infer processes such as limited dispersal, adult density, and colonisation history [4, 41].

The relative contribution of pollen and seeds to gene dispersal can be quantified using spatially explicit analyses – for example, based on parent-offspring patterns and *SGS* conditioned by effective population density – which allow effective dispersal distances to be estimated and demographic processes to be distinguished from microevolution [7]. *SGS* typically reflects greater genetic similarity between neighbours than between distant individuals, resulting from restricted dispersal, inbreeding and self-pollination; in the balance between dispersal and drift, this pattern can be modelled under the theory of isolation by distance (*IBD*). Conversely, large populations with high spatial connectivity tend to show weak or absent *SGS* [10].

The preservation of genetic diversity is critical in fragile biomes such as tropical ones, where fragmentation and habitat loss are particularly intense; approximately a quarter of global forest landscapes show increasing trends of fragmentation, with impacts in tropical and subtropical regions [13]. These alterations threaten the viability of species by eroding genetic diversity, reducing reproductive capacity, and limiting adaptive potential in the face of environmental change [21, 33].

Swietenia spp. (mainly *S. macrophylla*, *S. humilis,* and *S. mahagoni*) represent a critical case of conservation and forest management interest in the Neotropics: mahogany is one of the most valuable hardwoods and, due to overexploitation and habitat destruction, its populations are highly vulnerable [16, 24]. *S. mahagoni* pollination is mainly entomophilous: thrips have been described as important pollinators in this species, and bees and

moths are also cited as visitors/pollinators; therefore, pollen movement depends on the behaviour and mobility of these insects, with dispersal events of >1 km being recorded, depending on the landscape context and disturbance [9, 17]. The fruits are woody capsules containing 40-60 winged seeds; in *S. mahagoni*, capsules measuring ~8-10 × 4-6 cm and seeds measuring 5-6 cm have been reported, with dispersal mainly by wind. It has been indicated that the seeds can reach up to ~500 m from the parent tree. The production of viable seeds tends to be concentrated in dominant/codominant trees, and sexual regeneration may be limited by variable germination rates (10-70%), which affects their management and conservation [15]. In addition to its local socio-economic importance (artisanal use and furniture) and international commercial importance (high-value products), the conservation of *Swietenia* is central to sustainable management strategies in tropical regions [26, 27]. This intensive exploitation has led to severe fragmentation and a marked reduction of the natural habitat of these species, which have been listed as threatened under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) since 2002 [5]. Taken together, these pressures undermine the availability and long-term maintenance of genetic resources in mahogany species [5].

Currently, studies on *S. mahagoni* are insufficient to comprehensively assess genetic diversity, population structure, and spatial genetic structure using nuclear markers, which limits the design of robust conservation strategies [32]. In this context, the present study aimed to evaluate the nuclear genetic diversity and the *SGS* of two naturally established Cuban populations of *S. mahagoni*. We characterised: *i)* the level of nuclear genetic diversity in the species, and *ii)* how their fine-scale spatial genetic structure reflects stand establishment after the cessation of previous land uses. By characterising the small-scale *SGS* in naturally established populations of Cuban mahogany, this study will provide information for the design of conservation practices and the management of *S. mahagoni* genetic resources in Cuba.

2. Materials and Methods

2.1. Study Sites

Two naturally established Cuban populations of *S. mahagoni* were sampled in the province of Sancti Spíritus, Cuba (Table 1 and Figure 1). The two natural settlements of *S. mahagoni* stands – identified as the Modelo (SM-B) site and the Guira (SG-A) site – are remnants of heavily disturbed forest that was historically converted to agricultural and livestock use; natural regeneration began between 1993 and 1995, so the current cohorts are over three decades old. The average height (mean ± SD) was 9.84 ± 2.51 m in SG-A and 10.03 ± 1.63 m in SM-B.

2.2. Sample Collection

A total of 160 mature trees were surveyed with a minimum distance between trees of 2 m, distributed as shown in Table 1. The selected leaflets were preserved in silica gel for genetic analysis where upon they were stored in a freezer at -60°C until used for DNA extraction.

Sampled populations in Cuba Table 1

Population	Species	Region	Ab.	Latitude/ Longitude	Altitude [m]	N	Ft
Stand A	*S. mahagoni*	Guira	SG-A	21.78942/ -79.64634	60	80	Ne
Stand B	*S. mahagoni*	Modelo	SM-B	21.89687/ -79.41949	5	80	Ne

Note: Abbreviation (Ab.). Region of the sample in Sancti Spiritus, Cuba. Population (Pop.); species (Sp.); sample size (N); forest type (Ft): naturally established (Ne).

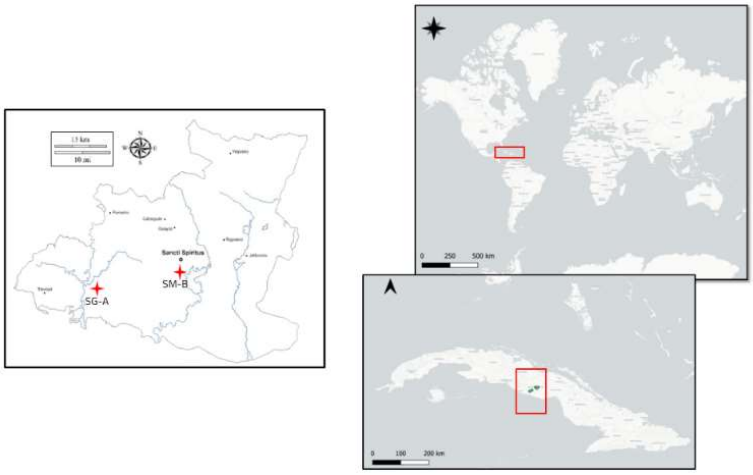

Fig. 1. *Geographical location of the studied stands in Cuba, where SG-A (Guira) and SM-B (Modelo)*

2.3. DNA Extraction, Amplification, and Sizing

Genomic DNA extraction was performed using the CTAB protocol [8], with slight modifications adapted to the leaf tissue of tropical trees to optimise DNA yield and purity. DNA was quantified using NanoDrop 8000 (Thermo Scientific, Wilmington, USA, 2008) and the extracted DNA was stored at -20°C. Eight nuclear microsatellites Sm01, Sm31, Sm32, Sm40, Sm45, Sm46, Sm47, and Sm51 were used [15], organised into two multiplex reactions: I (Sm01, Sm31, Sm32, Sm40) and II (Sm45, Sm46, Sm47, Sm51). Each PCR was performed in 11 µL, with 7.5 µL of Qiagen Multiplex PCR Master Mix 2×, 0.3 µL of each primer (forward and reverse), 1.2 µL of RNase-free water, and 2 µL of DNA.

The amplification programme included an initial denaturation of 15 min at 95°C, followed by 30 cycles (94°C – 1 min, 55°C – 30 s, 72°C – 1 min) and a final extension of 20 min at 60°C. The amplified products were diluted and analysed on a GenomeLab GeXP genetic analyser using the Frag-3 method and the 400-size standard.

2.4. Genetic Data Analysis

Standard genetic diversity indices were estimated following the same workflow described in our companion manuscript (Rodriguez et al., submitted). Specifically, we report here the nuclear metrics: number of alleles per locus (*Na*), mean number of effective alleles (*Ne*), Shannon's Information index (*I*), observed heterozygosity (*Ho*), and expected heterozygosity (*He*); calculated on the nuclear dataset used in this study. Differences between ecotypes were assessed by AMOVA in GenAlEx v.6.5 [29, 30].

2.5. SGS Analysis

A spatial autocorrelation analysis was performed to evaluate the *SGS* within each population using the multivariate method of Smouse and Peakall [36], implemented in GenAlEx v.6.5 [29, 30]. Geographical distances between individuals were calculated from GPS-recorded latitude and longitude coordinates. To estimate the expected genetic similarity in the absence of spatial association, 999 random permutations were performed, and 95% confidence intervals for each r value were obtained using 1,000 bootstrap resamples. The *r* values were plotted using the paired distance classes option; in SG-A, eight classes were examined with a step of 25 m, and in SM-B, seven classes were considered with a step of 10 m. The intensity of the fine-scale genetic structure was quantified using the *Sp* statistic, calculated as $Sp = -b_F/(1 - F1)$ in SPAGeDi v1.5 [12], where *F1* is Nason's mean kinship coefficient [22] for all pairs in the first distance class and b_F is the slope of the regression of kinship coefficients against the natural logarithm of geographical distance [38]. The significance of the regression slope was assessed using 10,000 permutations.

3. Results

3.1. Genetic Diversity

Nuclear genetic diversity was high in both populations, with consistently elevated allelic richness, effective allele numbers, and heterozygosity across loci. SG-A showed slightly higher values than SM-B, but both populations exhibited similarly strong diversity patterns. A detailed table with locus-specific *Na, Ne, I, Ho,* and *He* values is provided in our companion manuscript (Rodríguez et al., submitted).

AMOVA and genetic differentiation parameters for S. mahagoni Table 2

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	p
Among populations	1	73.200	0.812	9	
Within populations	158	1297.113	8.210	91	0,001
Total	159	1370.313	9.022	100	

Note: Degrees of freedom (d.f.); Sum of squares (SS) and Mean square (MS).

Molecular variance analysis (AMOVA) revealed that the largest proportion of genetic variation in *S. mahagoni* was found within populations (91%), while only 9% was attributed to differences between populations (Table 2). The component of

variance between populations was significant (0.812; p = 0.001), indicating low but statistically significant genetic differentiation between the two populations analysed. Overall, the total variance reached a value of 9.022.

3.2. Spatial Genetic Structure

Spatial autocorrelation correlograms showed very low values for the genetic correlation coefficient *r* in both populations (Figure 2). In SG-A, *r* was slightly positive in the distance classes (25-75 m; $r \leq 0.012$) and negative in the intermediate classes (100-125 m; $r \geq -0.025$), with some occasional deviations that approached the limits of the 95% confidence intervals. In SM-B, *r* oscillated around zero in all distance classes (10-70 m; $-0.034 \leq r \leq 0.088$) and remained within the confidence intervals, indicating an approximately random distribution of genotypes and no detectable genetic clustering at the scale analysed.

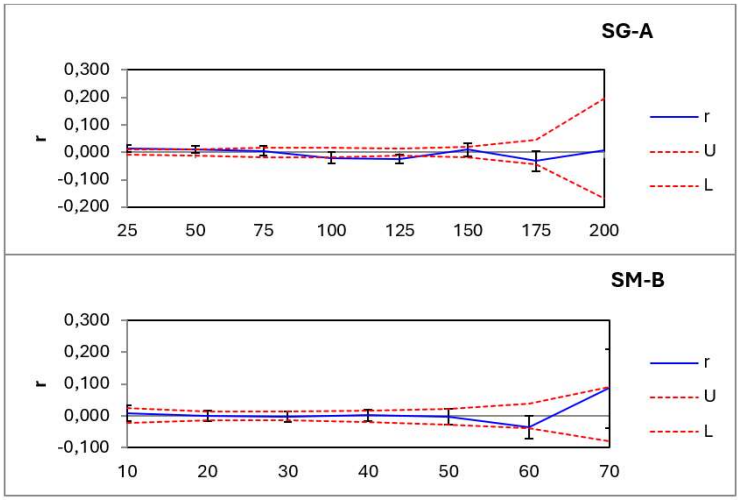

Fig. 2. *Multilocus spatial genetic correlograms of genetic and geographical distance in two populations of S. mahagoni. The y-axis is the genetic correlation coefficient (r), and the x-axis is the distance class (m); confidence intervals (95%) were calculated using permutation tests (red lines) and bootstrapped 95% confidence error bars around r are also shown; U – upper limit, and L – lower limit*

Table 3 shows the spatial genetic structure of both naturally established populations. In SG-A, the kinship coefficient in the first distance class was low and positive (*F1* = 0.0074), while in SM-B it was practically zero (*F1* ≈ 0). The kinship between the closest neighbours (*F1*) was close to zero in both populations (SG-A: 0.0074; SM-B: −0.0002). Consistently, the slope of the regression of kinship on the logarithm of distance was weakly negative and of low magnitude (SG-A: $b_F = -0.0109 \pm 0.0205$; SM-B: $b_F = -0.0111 \pm 0.0207$), indicating a barely perceptible decrease in kinship as distance increases. Consequently, the intensity of the spatial genetic structure was equally low in both stands, with virtually identical *Sp* values

(SG-A: 0.0110; SM-B: 0.0111). *Sp* ≈ 0.011 in both populations indicates a weak spatial structure; however, global permutation tests of the regression slopes were not significant (two-sided p > 0.5), so no consistent FSGS was detected at the scale analysed.

Parameters of the spatial genetic structure Table 3

Population	F_1	b_F (b-log) (±SE)	Sp = - $b_F/(1 - F_1)$
SG-A	0.0074	-0.0109 ± 0.0205	0.0110
SM-B	-0.0002	-0.0111 ± 0.0207	0.0111

Note: F1 is the average coefficient of relatedness between individuals of the first distance class); bF (b-log) – the slope of the regression of the coefficient of relatedness Fij; *Sp* – Intensity of the spatial genetic structure; SE – standard error.

4. Discussion

4.1. Genetic Diversity

As detailed in our companion manuscript (Rodriguez et al., submitted), the two natural populations of *S. mahagoni* in Cuba exhibit distinct nuclear genetic diversity (*Na* ≈ 12–13; *He* = 0.73-0.78). This level of variation suggests sufficient marker resolution for the analyses performed in this study. For example, in *S. macrophylla* in the Brazilian Amazon, an average of ≈9.5 alleles per locus and generally lower He values (≈0.47-0.64 per population) were found, although also indicative of high variability [18]. In populations of *S. macrophylla* in Mexico, subjected to varying degrees of selective exploitation, He values typically range between 0.65 and 0.78, with a slightly lower average number of alleles per locus than that observed in our study [1]. Recently, significantly lower levels of diversity (*Na* = 6.9; *He* = 0.43) have been reported in remaining populations of *S. macrophylla* in Ecuador, associated with the historical overexploitation of the species in that country [19]. Compared to this set of studies, the Cuban populations of *S. mahagoni* analysed herein stand out for maintaining a rich allelic pool and high expected heterozygosity, despite having established themselves naturally after the abandonment of previous land uses.

In turn, a study of five broadleaf species in Lithuania, revealed that naturally regenerated populations in areas affected by disturbances or land use changes retained levels of genetic diversity comparable to those of mature parent stands, highlighting the potential of these regeneration systems to maintain genetic variability [39]. Our results align with this idea and show that populations of *S. mahagoni* established naturally after the cessation of agricultural or forestry activities may constitute valuable genetic reservoirs.

In accordance with what was reported in our companion manuscript, F_{IS} was positive in both populations, which is consistent with a certain degree of non-random mating and/or local kinship. This is consistent with observations in other tropical outcrossing species, where recruitment from small reproductive neighbourhoods and limited pollen dispersal generate kinship correlations between nearby individuals and detectable heterozygote deficits with SSR markers [2, 6].

The AMOVA analysis showed that 91% of genetic variation occurs within populations and only 9% between the two populations

analysed. This partitioning of variation is consistent with what has been described for numerous long-lived woody species, including threatened tropical species. For example, in *Caryocar brasiliense*, a neotropical tree from the Cerrado, it was they found that ≈80-90% of the variation was distributed within populations, with relatively low but significant differentiation between populations [6]. Similarly, in *Saraca asoca*, a threatened medicinal tree in South Asia, the proportion of variation within populations was reported to be around 89-91% [37], close to that observed in our study. In S. macrophylla, both in the Amazon and Mesoamerica, SSR-based studies indicate that most diversity is maintained within populations, with FST (Fixation Index) or ΦST (Phi-statistic for population differentiation) around 0.08-0.10 [28], values comparable to the variance component between populations detected herein for *S. mahagoni*.

4.2. Fine Scale Spatial Genetic Structure

Although *Sp* ≈ 0.011 indicates a weak spatial structure, global permutation tests of the regression slopes were not significant ($p > 0.5$). Therefore, we did not detect a statistically significant and consistent FSGS at the scale analysed. The magnitude of *Sp*, however, is compatible with a slight aggregation of related genotypes at short distances, which can reflect limited seed-mediated gene flow [11, 36]. Still, the general pattern observed in the correlograms, with low (*r*) and, in many cases, insignificant genetic correlation coefficients, suggests that this structure is tenuous and does not manifest itself strongly at the spatial scale evaluated. Such a pattern – low *Sp* values combined with weak or inconsistent *r* – Is commonly reported in tropical, outcrossing species with moderate-to-high dispersal capacity [38].

Studies on other long-lived tropical tree species have reported similar or even lower *Sp* values. For example, *Dalbergia nigra* has *Sp* ≈ 0.017 [34], *Protium spruceanum* has *Sp* ≈ 0.008 [7], *Pouteria reticulata* between 0.006 and 0.010 [35], and *Carapa guianensis Sp* ≈ 0.004-0.005 [29]. In all these cases, the SGS is weak but detectable, reinforcing the idea that *Sp* values close to 0.01 are typical in long-lived tropical trees with allogamous reproductive systems and dispersal by animals or wind.

In SG-A, a barely positive signal was observed in the first classes, followed by slightly negative values at intermediate distances, while in SM-B it fluctuated around zero throughout the entire range evaluated. This contrast suggests that, if there was any initial family aggregation during establishment, it was very weak and/or it was quickly diluted by the mixing of seed and pollen sources. In turn, our results contrast with those described for the species *S. macrophylla* in Costa Rica, where a significant fine spatial structure was reported and attributed mainly to the limited range of seed dispersal and to the fact that many pollinations come from nearby trees [24].

Furthermore, in the case of *Swietenia* species, it has been explicitly pointed out that in open or cleared habitats (a typical situation after land abandonment/clearing), seed dispersal can be more extensive than in forests, increasing spatial mixing and reducing detectable *SGS* [17, 26]. In turn, other studies have found random *SGS* and maintained diversity in naturally established stands following changes in

land use [39]. From a conservation and sustainable management perspective, a weak *SGS* is a practical advantage, as it reduces the likelihood that seed collection or genetic sampling will be biased by "family clusters" of closely related individuals at the operational scale.

5. Conclusions

Nuclear *SGS* showed that two naturally established populations of *S. mahagoni* in Cuba maintain high genetic diversity, with no signs of severe erosion following the cessation of previous land uses. At a fine scale, *SGS* was weak or almost absent, consistent with post-abandonment establishment influenced by multiple seed sources and effective gene flow, which limits the formation of detectable family groupings. For conservation and sustainable management, these naturally regenerated stands represent key genetic reservoirs and potential seed sources for restoration. Their management should focus on maintaining many reproductive trees, preserving landscape connectivity, collecting seed in a representative manner, and sustaining long-term genetic monitoring to protect the diversity and adaptive capacity of *S. mahagoni*.

Acknowledgements

This work was funded by Transilvania University of Brasov. We would like to thank Ana G. Trocones Boggiano, Luis A. Delgado Fernández, and Jorge F. Lorenzo Évora (colleagues from the University of Sancti Spiritus "José Martí", Cuba) for their kind assistance in collecting the specimens for this study.

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