Genetic structure and genetic diversity of *Swietenia macrophylla* in areas subjected to selective logging in Quintana Roo, Mexico

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Abstract: The hypothesis that selective logging has a negative effect by altering the genetic parameters of tropical tree species was evaluated. The genetic diversity and genetic structure between adult trees ($N = 47$) and saplings ($N = 50$) of *Swietenia macrophylla* were contrasted within an area subjected to selective logging in the Mayan zone. Although differences in the number of alleles and in their frequencies were detected between both groups, the observed and expected heterozygosity and the coefficient of fixation were statistically similar. Evidence of higher genetic structure in the group of saplings was revealed by both, the autocorrelation and the factor correspondence analyses. The genetic differences observed in this study are compatible with those expected under scenarios of disruption in the local pattern of gene flow produced by selective logging. The implication of these results on the conservation genetics of *Swietenia macrophylla* in the Mayan zone is discussed.

Keywords: autocorrelation analysis, big-leaf mahogany, conservation genetics, Moran's index, tropical timber species.

Resumen: Se evaluó la hipótesis de que la tala selectiva genera un efecto negativo alterando los parámetros genéticos de las especies de árboles tropicales. Se contrastó la diversidad genética y la estructura genética entre árboles adultos ($N = 47$) e individuos juveniles ($N = 50$) de *Swietenia macrophylla* en una zona sujeta a la tala selectiva en la zona maya. Aunque se detectaron diferencias entre ambos grupos de árboles en el número de alelos y en sus frecuencias, la heterocigosis observada y la esperada, y el coeficiente de fijación fueron estadísticamente similares. Análisis de autocorrelación espacial y factorial de correspondencias mostraron una mayor estructura genética en el grupo de individuos juveniles. Las diferencias genéticas observadas en este estudio son compatibles con las esperadas bajo escenarios de perturbación en el patrón local del flujo de genes producto de la tala selectiva. Se discute la implicación de estos resultados en la conservación genética de *Swietenia macrophylla* en la zona maya.

Palabras clave: análisis de autocorrelación espacial, caoba de hoja grande, conservación genética, especies tropicales maderables, índice de Morán.

Biodiversity is currently threatened, directly or indirectly by human activities in almost all terrestrial habitats. Due to this, in conservation biology it is important to understand how species respond to anthropic disturbances (Sih *et al*., 2000; Cushman, 2006). This challenge is particularly relevant for tropical forests because these biomes sustain both, high species richness and a high level of human-induced disturbance (Lowe *et al*., 2005; Wright and Muller-Landau, 2006). Tropical trees are expected to be particularly susceptible to changes in habitat characteristics because of their

low population density (ca. one reproductive tree × ha⁻¹), self-incompatibility systems and their frequent dependence on animals for pollination (Cunningham, 2000; Lowe *et al*., 2005; Dick *et al*., 2008).

The selective logging of target trees with the best characteristics is the commonest strategy in most tropical forests subjected to legal harvesting (Jennings *et al*., 2001; Sist *et al*., 2003; Asner *et al*., 2005; Biscaia-de Lacerda *et al*., 2008). Selective logging is conceived as a sustainable strategy of forest management due to its intensity is based

on growth rates (Snook, 2003; Shono and Snook, 2006). However, it has been proposed that selective logging could impact directly on the local pattern of gene makeup as it tends to reduce population size and/or population density and because it increases the distance between reproductive individuals (Sebbenn *et al*., 2008). Therefore, the extraction of reproductive trees subsequently reduces outcrossing rates (Murawski *et al*., 1994; Lee, 2000; Obayashi *et al*., 2002), increases inbreeding (André *et al*., 2008) as well as the extent of genetic differentiation (Degen *et al*., 2006; Cloutier *et al*., 2007; Biscaia-de Lacerda *et al*., 2008; Sebben *et al*., 2008; Silva *et al*., 2008).

Swietenia macrophylla King in Hook is undoubtedly the most important timber species in Neotropics. It has being traded along its entire geographic distribution, which ranges from the Amazon Basin to South Mexico (Snook, 1998). In Mexico, *S. macrophylla* has been logged since the late 19th century. With the implementation of federal regulations (Plan Piloto Forestal) by the 1980s the harvesting plans performed in the so-called Mayan zone (central part of Quintana Roo), included initial inventories and the determination of growth rates. Currently, the management plan is based on polycyclic harvesting with 25-y cutting cycles and a minimum cutting diameter of 55 cm (Bray *et al*., 2003).

An important consequence of the extraction of largest individuals for timber is that regeneration relies on small-size remnant trees (Gutiérrez-Granados and Dirzo, 2009). As a result, natural regeneration could be limited by a low fruit production, restricted seed shadow, increased seed predation, and a high rate of herbivory in young ontogenetic stages (Snook *et al*., 2005; Cámara-Cabrales and Kelty, 2009; Gutiérrez-Granados *et al*., 2011). However, studies addressing the effects of selective logging on genetic parameters are currently absent for Mexican populations of *S. macrophylla*. If selective logging is exerting some effect on population dynamics, we expect to find genetic differences between the group of adult trees and that derived by the natural regeneration. In particular, it is predicted a higher spatial genetic structure (i.e., higher genetic relatedness at short distances) and lower genetic diversity in saplings rather than in adult trees.

Materials and methods

Study site. Fieldwork was carried out in the ejido (communal owned lands) named Señor X-Maben, that is located in the municipality of Felipe Carrillo Puerto (19° 00' - 20° 00' N and 88° 00' - 88° 20' W; Figure 1). The predominant vegetation is tropical moist forest (*sensu* Holdridge, 1967), with intermingled patches of savanna and flooded forest (Gutiérrez, 2010). Tree species as *Brosimum alicastrum* Sw., *Bursera simaruba* (L.) Sarg., *Cedrela odorata L., Caesalpinia mollis* (Kunth) Spreng., *Coccoloba spicata* Lundell, *Cordia dodecandra* DC., *Lysiloma bahamense* Benth., *Manilkara*
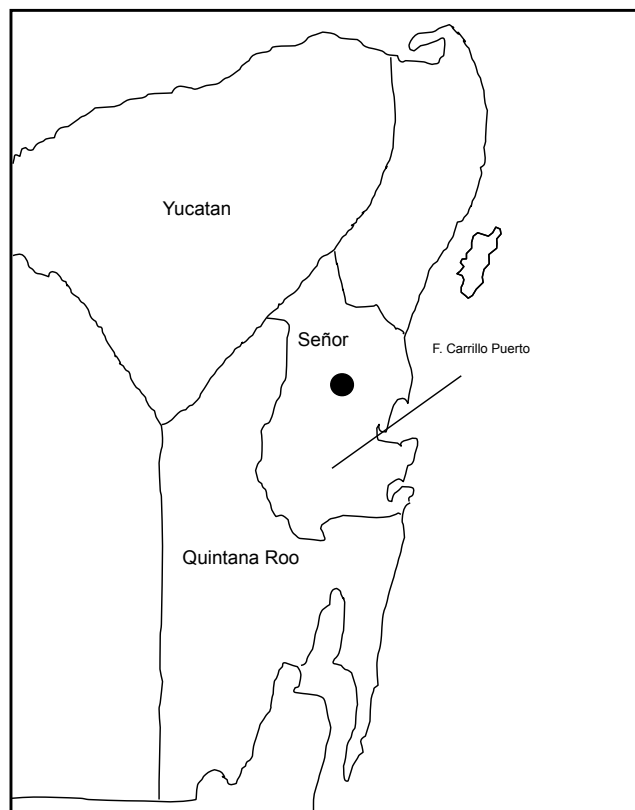
Figure 1. Location of the study site (Señor) within the municipality of Felipe Carrillo Puerto in Central Quintana Roo, Mexico.

zapota (L.) Royen, *Metopium brownei* Urb., *Piscidia communis* Harms, *Platymiscium yucatanum* Standl. and *Pouteria reticulata* (Engl.) Eyma are also present in the zone (Rebollar-Domínguez *et al*., 2002; Vester and Navarro-Martínez, 2005).

Sampling design. Some studies sampling only adult trees have shown an apparent absence of negative effects of selective logging, forest fragmentation or deforestation on genetic parameters. This result has been explained by considering these anthropic disturbances as relatively recent processes with regard to the long-life span of adult trees (White *et al*., 1999; Collevatti *et al*., 2001; Lowe *et al*., 2005). Therefore, a more informative approach has been derived from the genetic comparison between adults and their regeneration, assuming that the disruption of processes affecting gene flow between adult trees (i.e., pollination) should produce measurable effects on progeny.

Genetic analyses were performed on 47 adult trees and 50 saplings of *Swietenia macrophylla* located within a 600-ha forest surface subjected to a first cutting cycle in 1998. Originally 160 individuals were mapped in the area; however, individuals separated from each other by at least 100 m were selected in order to avoid the probability of sampling within genetic families (Gillies *et al*., 1999; Navarro *et al*., 2010).

Diameter at breast height (DBH 1.30 m) of adult trees ranged from 35 to 45 cm, whereas height of saplings was < 50 cm. For adult trees, a slingshot was used to obtain leaves from the upper part of the crown, whereas a telescopic pruner was used to sample at lower height. Only the leaves free of apparent damage by pathogens and insects were selected. The sampled tissue per plant was kept in previously marked sealed plastic bags containing blue indicator silica gel to stabilize DNA through a rapid desiccation of plant material.

DNA-procedures. Isolation of DNA was performed through a standard Cetyl Trimethyl Ammonium Bromide (CTAB)-based procedure (Doyle and Doyle, 1987). Quality of samples was improved by applying GENECLEAN®. A set of primers Sm01, Sm31, Sm47 and Sm51 were used from those developed for *Swietenia macrophylla* (Lemes *et al.*, 2002). The final reaction consisted of 15 μl total volume containing 1× PCR buffer, 1 mM $MgCl_2$, 0.2 mM dNTP's, 1 μL *Taq* DNA polymerase (Vivantis Technologies, Selangor, Malaysia) and 5 ng of template DNA. Amplification conditions for *primer* sm47 were: an initial denaturing step of 95 ℃ 1 min followed by 30 cycles of 95 ℃ 1 min, 56 ℃ 1 min and 72 ℃ 1 min, and a final extension step of 72 ℃ 10 min. For the other three primers the conditions were: an initial step of 94 ℃ for 3 min followed by 30 cycles of 1 min at 94 ℃, 1 min at 56 ℃, 4 min at 72 ℃ and an extension step of 72 ℃ 10 min. PCR products were subjected to electrophoresis in 6 % polyacrilamide gel in Tris-Borate Ethylenediaminetetraacetic acid (TBE) buffer. Gels were stained with ethidium bromide and photographed under UV light. Then, the different alleles for each locus were scored according to their molecular mass (White *et al.*, 2002; Céspedes *et al.*, 2003). The allele located closer to anode was arbitrarily identified as "1", and the remaining alleles were identified sequentially (Céspedes *et al.*, 2003).

Statistical analyses. The genetic differences between adults and saplings of *Swietenia macrophylla* were analyzed with four different approaches, allelic frequencies, heterozygosity-based information, autocorrelation analysis and factor correspondence analysis. For the allelic information, the total number of alleles found in the population, the number of alleles per locus and their respective allelic frequencies were described. In addition, the alleles present in eight frequency classes for adults and saplings were counted. The statistical differences between both groups were tested by a contingency table (Sokal and Rohlf, 1995). Second, the mean values for both the observed heretozygosity (H_O) and expected heterozygosity (H_E) were calculated using ARLEQUIN (Excoffier *et al.*, 2005). The coefficient of fixation (F_{IS}) that indicates departures of genotypic frequencies from Hardy–Weinberg equilibrium was also estimated. The significance of the coefficients F_{IS}, were tested using a Monte Carlo chain with 1,000 iterations (Excoffier *et al.*, 2005).

Genetic differences between adults and saplings regarding these tree estimates were evaluated performing independent Mann-Whitney tests (Sokal and Rohlf, 1995).

Third, three independent spatial autocorrelation analyses were performed to investigate differences between both groups in the fine-scale genetic structure (Degen *et al.*, 2001). The autocorrelation analysis has been used to identify a series of processes that affect the local pattern of gene flow and that consequently shape the fine-scale genetic structure (Smouse and Peakall, 1999; Degen *et al.*, 2001; Vekemans and Hardy, 2004). The spatial autocorrelation analysis performed on the molecular information evaluates if the pairwise genetic relatedness varies depending on the separation distance of the compared individuals. From this relationship, a spatial random distribution is expected as a null hypothesis. Instead, a higher genetic relatedness at shorter distances is expected under conditions restricting gene movement.

The SGS software utilized in this study to perform the autocorrelation analyses returned correlograms displaying the variation in the magnitude of the Moran's Index (genetic relatedness) obtained for multilocus genotypes according with the separation distance of pairs of individuals. Along the *x*-axis of the correlograms, the variation in the separation distance between compared individuals is displayed in the form of ranges (distance classes; Degen, 2000). A permutation procedure using Monte-Carlo simulations was applied to test for significant deviation from the spatial random distribution. For each one of the spatial distance classes, observed values were compared with the distribution obtained after 1,000 permutations. Then, a 95 % confidence interval for the parameters was obtained. Thus, positive values of Moran's Index located beyond the confidence limit represent statistically significant deviations of the random distribution (positive fine-genetic structure). The consistency of the genetic spatial pattern was evaluated varying the number of distance classes. To do this, three analyses per group were performed using 5, 7, and 15 distance classes. In all cases, at least 30 pairs of data points per distance class were used (Degen, 2000).

Finally, a factorial correspondence analysis was carried out using GENETIX 4.05.2 (Belkhir *et al.*, 1996-2000). With this analysis, the genetic structure was qualitatively examined by comparing the extent of genetic variation displayed for both groups in a multivariate space. A strong overlapping in the distribution pattern between adults and saplings would indicate the absence of genetic differences between them.
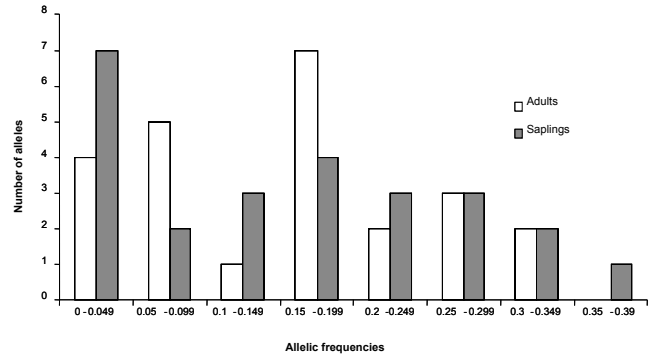
Results

Genetic diversity. The information extracted from the four loci utilized in this study revealed a total of 25 alleles. The genetic polymorphism varied lightly among loci. The lowest

Table 1. Allelic frequencies for adults and saplings of *Swietenia macrophylla* per microsatellite locus.

Locus	Adults	Saplings
Sm22	Allelic frequencies	
1	0.1625	0.2708
2	0.2625	0.2396
3	0.0500	0.1563
4	0.325	0.1979
5	0.2000	0.1354
Sm31		
1	0.0556	0.0301
2	0.0778	0.0000
3	0.1889	0.0602
4	0.3001	0.3711
5	0.2111	0.2311
6	0.1666	0.3102
Sm47		
1	0.0465	0.0417
2	0.0465	0.0418
3	0.1861	0.2083
4	0.1863	0.1875
5	0.1861	0.3229
6	0.2791	0.1979
7	0.0698	0
Sm51		
1	0.0349	0.0106
2	0.1512	0.0957
3	0.0233	0.1277
4	0.3023	0.2979
5	0.0814	0.0319
6	0.2791	0.2872
7	0.1279	0.1489

Figure 2. Differences in allelic frequencies between adults and saplings of *Swietenia macrophylla*.

($\chi^2 = 23.37$, df = 7, $P = 0.0014$, Figure 2). Differences were present in most of the frequency categories, in particular on alleles at frequencies < 0.25 (Figure 2). With regard the genotypic information, in both groups, the observed heterozygosity (H_O) was markedly lower than expected heterozygosity (H_E) for all loci. In consequence, positive values for the coefficient of fixation (F_{IS}) were obtained that indicate a statistically significant deficiency of heterozygotes (Table 2). No statistical differences in H_O, H_E, and F_{IS} between adults and saplings were detected by the independent Mann-Whitney tests (Table 2).

Genetic structure. The three autocorrelation analyses performed for both adults and saplings showed consistent results. This means that the relationship between the genetic relatedness of individuals with spatial distance was not affected by the variation in the number of distance classes (5, 7 or 15). No departures from a random pattern were detected in the analysis corresponding to adults. This is because the values for the Moran´s Index were constrained within the confidence limits along the variation in the separation distance between compared individuals (Figure 3). In contrast, a statistically significant fine-scale genetic structure was observed for saplings. In this group, positives values of the Moran´s Index (ca. 0.05 of magnitude) were situated beyond the confidence limit along the first 1,000 m of separation distance (Figure 3). This indicates the occurrence of individuals that are more genetically related than the expected by random.

number of alleles (5) was observed for locus Sm22, whereas loci Sm51 and Sm 47 revealed the occurrence of seven alleles (Table 1). In the group of adults, 21 alleles showed a frequency equal or higher to 0.05. In contrast, in the group of saplings seven alleles showed a low frequency (< 0.05). In fact, two alleles present in adult trees were absent in that group, whereas all alleles present in saplings were detected in adult trees.

The analysis of the distribution of allelic frequencies showed significant differences between adults and saplings

Table 2. Observed heterozygosity (H_O), expected heterozygosity (H_E) and coefficient of fixation (F_{IS}) for adults and saplings of *Swetenia macrophylla*.

Locus	Adults			Saplings		
	H_O	H_E	F_{IS}	H_O	H_E	F_{IS}
Sm22	0.3861	0.7923	0.5128	0.2979	0.7884	0.6222
Sm31	0.5348	0.8186	0.3446	0.5417	0.7827	0.3079
Sm47	0.5777	0.7981	0.2782	0.2801	0.7168	0.6094
Sm51	0.2075	0.7661	0.5986	0.2625	0.7956	0.6701
Mean	0.4516	0.7938	0.4335	0.3455	0.7709	0.5524
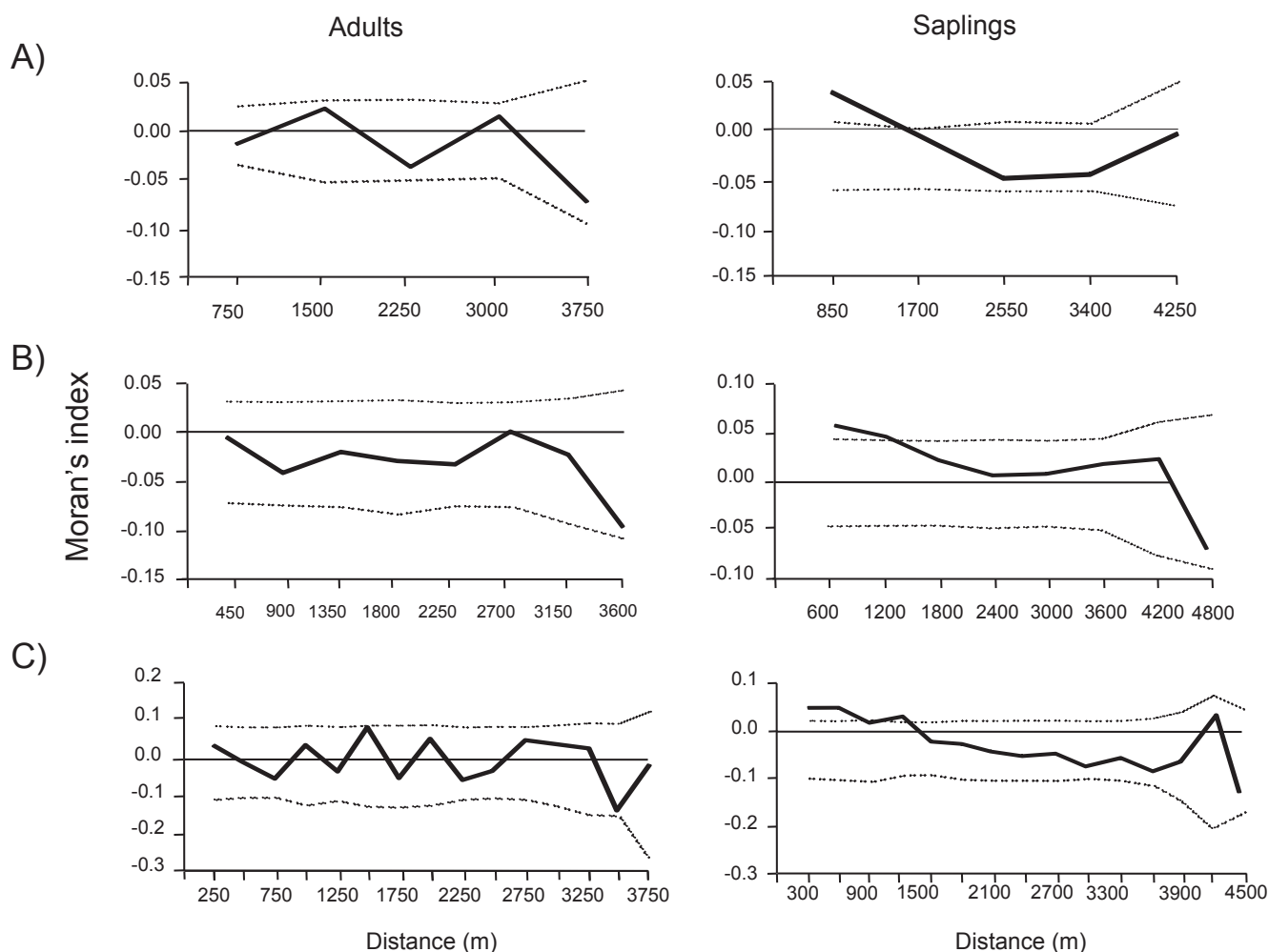
Figure 3. Correlograms for adults (left) and saplings (right) of *Swietenia macrophylla* showing the relationship of the Moran´s Index (D, continuous line ± 95 % CI broken lines) with the separation distance between pairs of individuals. Significant values of Moran's Index are those situated beyond the CI.

The information summarized by the first two axes derived from the factorial correspondence analysis explained 37 % of the total variance and showed genetic differences between adults and saplings (Figure 4). In this multivariate space, the scores of saplings along Axis 1 were constrained between -0.7 and 0.7. In contrast, the scores of adult trees ranged between -1 and 1.5 for the same Axis 1. The coefficients of adults also showed a higher variation on the Axis 2 (Figure 4).

Discussion

The management implemented in the Mayan zone has received international acknowledgement as a low impact, socially fair and a community-based forestry program (Bray *et al.*, 2003). However, recent ecological evidence obtained for *Swietenia macrophylla* indicates the existence of negative effects of selective logging on different components related with its natural regeneration. For example, selective

logging limits fruit production (Snook *et al.*, 2005), seed dispersal (Cámara-Cabrales and Kelty, 2009) and increase both, the risk of herbivory and seedlings mortality (Gutiérrez-Granados *et al.*, 2011). In accordance with our prediction, the genetic differences detected in this study between adults and saplings of *S. macrophylla* are compatible with those expected under conditions of selective logging.

Genetic diversity. Overall, our results were similar to those reported for other Mexican populations of Swietenia macrophylla sampled within the Yucatan peninsula and analyzed with microsatellite loci. For example, Trujillo-Sierra *et al.* (2013) reported from 21 to 26 alleles per population (29 alleles in total), whereas 25 alleles were reported in this study (in the group of adults for comparison). Mean values of the observed heterozygosity (H_O) of 0.420 and 0.410 has been reported respectively by Trujillo-Sierra *et al.* (2013) and by Alcalá *et al.* (2014), which coincide with our estimate of 0.451. These two studies also showed a statistically signifi-
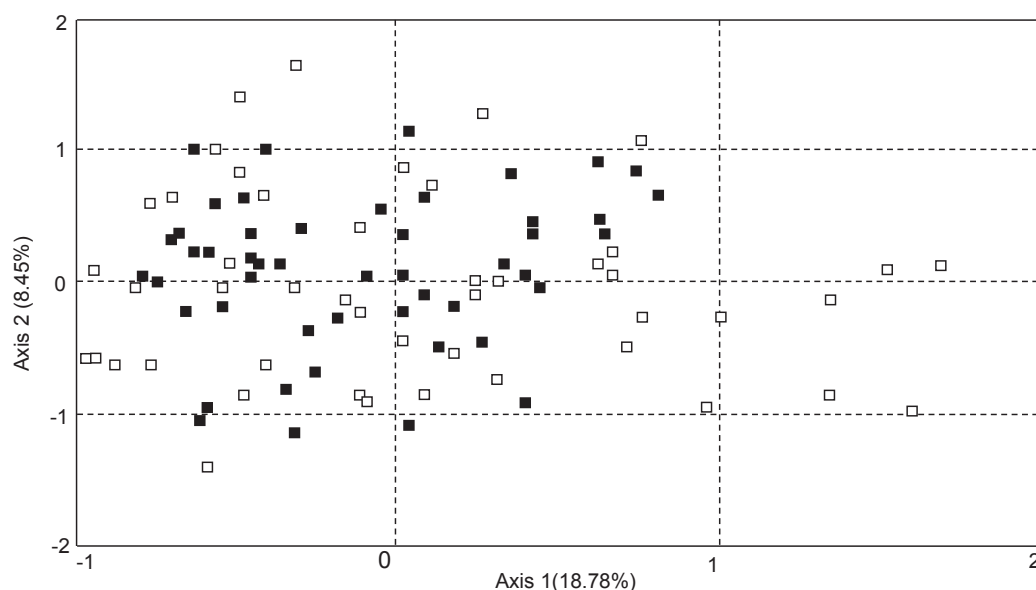
Figure 4. Biplot derived from the factorial correspondence analysis for *Swietenia macrophylla* (white markers = adults, black markers = saplings).

cant deviation of the genotypic frequencies, revealing a high coefficient of fixation (0.309 and 0.449, respectively). In this study, a mean value for the F_{IS} was 0.43. All the results involving allelic and genotypic information indicate that Mexican populations could maintain overall low levels of genetic diversity and high scores for the coefficient of fixation by historic reasons. This is because there is evidence that suggests that northern populations of *Swietenia macrophylla* maintain lower heterozygosity due to the colonization toward northern latitudes from South America (Lemes *et al.*, 2003, Novick *et al.*, 2003), a pattern that is still observed along the distribution of this species in Mexico (Alcalá *et al.*, 2014).

Statistically significant differences between adults and saplings were detected for the number of alleles present at different frequency categories. In fact, saplings of *Swietenia macrophylla* showed lower polymorphism, lacking of two alleles that were present in adult trees. These results are similar to the reported for other tree species subjected to selective logging (Rajora *et al.*, 2000; Silva *et al.*, 2008). Interestingly, no statistical differences between adults and saplings of *S. macrophylla* were found for the mean values of H_O, H_E, and the coefficient of fixation (F_{IS}). Although a clear reduction in H_O and a statistically significant increase in the coefficient F_{IS} have been reported for *S. macrophylla* as a result of selective logging (André *et al.*, 2008), most studies in other tree species have not reported at a short-term, genetic differences between logged and unlogged populations (Rajora *et al.*, 2000; Cloutier *et al.*, 2007; Sebbenn *et al.*, 2008; Silva *et al.*, 2008), fragmentation and habitat degradation (Lowe *et al.*, 2005), and even at a long-term as revealed by simulation models (Young *et al.*, 1996; Degen *et al.*, 2006; Sebbenn *et al.*, 2008). Therefore, although changes in al-

lelic frequencies and loss of rare alleles produced by selective logging have been commonly detected (Rajora *et al.*, 2000, Silva *et al.*, 2008, this study), heterozygosity seems to be highly resilient to the reduction in population size. This is because under neutrality, the theoretically per generation rate of loss of heterozygosity is set at 1/2Ne (Franklin, 1980). At this rate, population reductions should occur at a very high magnitude to produce marked reductions, as the loss of rare alleles (those that are lost first) shows a limited effect on this parameter in the short-term (Hedrick, 2000). However, the absence of differences in heterozygosity between adults and saplings may be explained by the overall low levels of genetic diversity that Mexican populations sustain as a result of the expansion of its geographic range, as explained above (Lemes *et al.*, 2003, Novick *et al.*, 2003; Alcalá *et al.*, 2014).

Genetic structure. The occurrence of a fine-scale genetic structure has been commonly detected in plant populations through the implementation of autocorrelation analysis. In particular, some ecological factors affecting local patterns of gene movement have been advanced to explain the fine-scale genetic structure observed in tropical trees. For example, in adults of *Dicorynia guianensis* Amshoff the within-population genetic structure resulted from tolerance to selfing, overlapping generations or selection (Latouche-Hallé *et al.*, 2004). In adults of *Swietenia macrophylla* (Lowe *et al.*, 2003) and *Simarouba amara* (Hardesty *et al.*, 2005) autocorrelation resulted as a consequence of restricted seed dispersal, whereas in *Bagassa guianensis* Aubl. the genetic structure was due to biparental inbreeding (Silva *et al.*, 2008).

In this study, no evidence of fine-scale genetic structure in the group of adult trees was found. However a positive genet-

ic structure was found in the group of saplings. The genetic information of adult trees (not deviated from a random pattern) may represent conditions of higher gene flow that were present before or very close to the implementation of the first cutting cycle in the stand (ca. 16 years ago). Consequently, the positive spatial autocorrelation observed in saplings is interpreted as evidence of disruption in the local pattern of gene flow probably produced by selective logging.

Even under random mating, in conditions of limited seed dispersal it can be expected an increase in relatedness at decreasing spatial scales (Vekemans and Hardy, 2004). Seeds of *Swietenia macrophylla* remain viable for only few months, so seedlings present in the area have resulted unequivocally from seeds recently produced. Therefore, progeny could reflect the occurrence of current ecological conditions that affect gene admixture in sites subjected to selecting logging. For example, it has been documented that small-remnant trees of *S. macrophylla* in the Mayan zone seems to show a limited seed dispersal (Cámara-Cabrales and Kelty, 2009). So the higher genetic relatedness in the group of saplings should be linked to the limited seed dispersal caused by selective logging. This is because the progeny has been produced mainly by small and nearby remnant trees, as the largest individuals have been almost entirely removed (Santos-Jiménez *et al*., 2005).

In addition, a restricted gene movement could also be explained by a limited pollen movement, as anthropogenic activities have the potential to disrupt mutualistic interactions. First, changes in behaviour of pollinators affecting reproductive success in tropical trees have been detected in disturbed forests (Ghazoul *et al*., 1998; Ghazoul and McLeish, 2001). Second, outcrossing rates may be also diminished by a reduction in the proportion of flowering trees in logged forests (Murawski and Hamrick, 1991; Murawski *et al*., 1994; Obayashi *et al*., 2002). Third, the average effective number of pollen donors and the number of sires per mother were lower in isolated patches than in continuous forests (Rosas *et al*., 2011). These three effects suggest that in our study, saplings could have been derived from a subset of adult trees, whereas a higher number of reproductive individuals were involved in the production of current adult trees. Therefore it seems that both, the alteration of the interaction with pollinators and the limited seed dispersal produced by selective logging could be involved in the higher genetic structure observed in the group of saplings (Lourmas *et al*., 2007).

The results derived from the autocorrelation analyses were supported by the results obtained from the factorial correspondence analyses that indicated a higher genetic structure within the saplings groups. Although the factorial correspondence analysis is not an explicit spatial approach to test for genetic structure, it showed that the multi-locus genotypic variation of adult trees was twice as much as the observed in the group of saplings. This result agreed with the observed for other tropical tree species. For example, a reduction in the number of genotypes has been documented as a result of selective logging (Degen *et al*., 2006), whereas the number of mutilocus genotypes registered in seedlings was a half compared with those present in adult trees of *Swietenia macrophylla* located in a forest fragment of Brazil subjected to selective logging (André *et al*., 2008).

Conservation considerations. The magnitude of the Moran´s Index of about 0.05 obtained in the autocorrelation analysis has been observed commonly among tropical tree species. However, the positive autocorrelation found in the group of saplings at distances of up to 1,000 m has not been frequently reported in literature. The widespread signal for the spatial genetic structure in saplings and the high coefficient of fixation of about 0.4, indicate mating among relatives probably produced by limits to gene flow via seed dispersal and pollen movement. These high values for the coefficient of fixation are important for the future conservation of populations, as the occurrence of inbreeding in naturally outcrossed species could conduce to the loss of fitness (Frankham *et al*., 2010). Therefore, studies addressing the fitness performance of progeny are a priority for the conservation of this species at the Mayan zone. However, it would be necessary for future studies to evaluate the genetic structure and genetic diversity considering more sites, as for example, the volume of wood removed and the areas set aside for logging greatly vary among different ejidos within the Mayan zone (Santos-Jiménez *et al*., 2005). To evaluate if adults of *Swietenia macrophylla* can be utilized as a control group (i.e., indicating conditions before the implementation of selective logging), the experimental design should include comparisons between adults and saplings in zones with and without selective logging.

The integration of ecological data available in literature with the genetic information about *Swietenia macrophylla* in the Mayan zone provided by this study, indicates that the current management program performed under the current conditions (i.e. 25-y cycles, minimum cutting diameter ≥ 55 cm), should be reviewed in order to assure not only natural regeneration, but the maintenance of genetic diversity. It is important to note that the genetic differences (loss of alleles, higher genetic structure) observed between adults and saplings in this study, are related to the implementation of the first cutting cycle, some 16 y ago. Therefore, future cutting cycles of adult reproductive trees could reduce the effective population size, which in consequence could produce higher negative impact on allelic richness and heterozygosity. The protection of several large individuals as pollen donors and seed sources should occur to increase gene flow and the effective population size. Large individuals are crucial to maintain the genetic diversity of the northernmost big-leaf mahogany populations, and the Mayan zone inhabitants' income as well.

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