Molecular Ecology (2003) 12, 2875–2883 doi: 10.1046/j.1365-294X.2003.01950.x

Population genetic structure of mahogany (*Swietenia macrophylla* King, Meliaceae) across the Brazilian Amazon, based on variation at microsatellite loci: implications for conservation

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Abstract

Mahogany (*Swietenia macrophylla*, Meliaceae) is the most valuable and intensively exploited Neotropical tree. No information is available regarding the genetic structure of mahogany in South America, yet the region harbours most of the unlogged populations of this prized hardwood. Here we report on the genetic diversity within and the differentiation among seven natural populations separated by up to 2100 km along the southern arc of the Brazilian Amazon basin. We analysed the variation at eight microsatellite loci for 194 adult individuals. All loci were highly variable, with the number of alleles per locus ranging from 13 to 27 (mean = 18.4). High levels of genetic diversity were found for all populations at the eight loci (mean H_E = 0.781, range 0.754–0.812). We found moderate but statistically significant genetic differentiation among populations considering both estimators of F_{ST} and R_{ST}, θ = 0.097 and ρ = 0.147, respectively. Estimates of θ and ρ were significantly greater than zero for all pairwise population comparisons. Pairwise ρ-values were positively and significantly correlated with geographical distance under the isolation-by-distance model. Furthermore, four of the populations exhibited a significant inbreeding coefficient. The finding of local differentiation among Amazonian mahogany populations underscores the need for *in situ* conservation of multiple populations of *S. macrophylla* across its distribution in the Brazilian Amazon. In addition, the occurrence of microgeographical genetic differentiation at a local scale indicates the importance of maintaining populations in their diverse habitats, especially in areas with mosaics of topography and soil.

Keywords: Amazon, conservation genetics, genetic structure, mahogany, microsatellites, *Swietenia macrophylla*, tropical tree

Received 24 March 2003; revision received 6 June 2003; accepted 10 July 2003

Introduction

The destruction of tropical forests world-wide has increased dramatically in recent decades (Whitmore 1997; Bawa & Seidler 1998), posing a significant threat to the maintenance of biodiversity and biological processes in tropical forest ecosystems (Bawa 1994; Young *et al.* 1996). The genetic threat to tropical trees results from the loss of genetic diversity associated with the extinction of local populations, reduced population sizes, and the disruption of mutualisms with pollinators and seed-dispersing animals (Bawa 1994; Hall *et al.* 1996; Nason *et al.* 1997; Aldrich *et al.* 1998; Dick 2001). Moreover, selective logging may promote dysgenic selection as a result of the continuous exploitation of large, superior individuals and may increase levels

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of inbreeding as a result of reduction in stand density (Bawa 1994; Murawski *et al.* 1994). To evaluate and mitigate the genetic effects of deforestation and logging, it has become a priority to obtain information on the natural levels and distribution of genetic variation in populations of tropical trees.

Population genetic studies of tropical trees have shown that most of the species investigated are outcrossed, exhibit high levels of genetic diversity and gene flow, and carry much of the variation within rather than among populations (Hamrick & Loveless 1989; Alvarez-Buylla *et al.* 1996). However, the great majority of these studies were developed over relatively small spatial scales, and employed isozymes as the primary genetic markers (Hamrick & Loveless 1986; Loveless 1992, 1998; Alvarez-Buylla & Garay 1994; Hall *et al.* 1994). In recent years, the development of microsatellites for an increasing number of tropical trees (White & Powell 1997; Aldrich *et al.* 1998; Brondani *et al.* 1998; Collevatti *et al.* 1999; Dayanandan *et al.* 1999; Dick & Hamilton 1999; Gaiotto *et al.* 2001; Lemes *et al.* 2002) have allowed larger scale and more refined studies of population genetic structure (e.g. White *et al.* 1999; Collevatti *et al.* 2001).

The central aim of this work was to characterize and understand the genetic structure of natural populations of mahogany (*Swietenia macrophylla*, Meliaceae) across a 2100-km transect of the Brazilian Amazon using microsatellite loci recently developed for this species (Lemes *et al.* 2002). Despite the perceived importance of the Amazon basin for tree species diversity, and as a repository for half the world's remaining rain forest, our investigation of mahogany is the first population genetic analysis of a tree species distributed across this vast region. Furthermore, mahogany is of considerable interest to resource managers as it is by far the most valuable Neotropical hardwood species. One cubic metre of export-quality sawn mahogany is valued at about US$ 700 on the international market (Verissimo *et al.* 1995), and Brazil alone exports about 500 000 m^3/year. A previous population genetic study of mahogany was limited to Central America where the species is commercially extinct in most regions (Gillies *et al.* 1999).

The recent inclusion of mahogany in CITES (Convention for International Trade in Endangered Species, Appendix II 2002) highlights international concern regarding the future of South American populations. Most natural populations of mahogany have been logged and there is evidence that the species does not regenerate in areas of intense exploitation (Gullison *et al.* 1996). Thus there is an urgent need for effective conservation and management of the remnant populations. To this end estimates of population genetic parameters are essential. The variability observed at microsatellite loci provides estimates of inbreeding, heterozygosity, gene flow and outcrossing rate, all of which are important measures for assessing the conservation and management status of tropical trees under intense human pressure.

The specific goals of our mahogany research were: (i) to quantify the genetic diversity within and among a sample of natural populations at the regional and topographic scale of the Brazilian Amazon; (ii) to test for the association between genetic and geographical distances among populations; and (iii) to provide recommendations for the establishment of *in situ* reserves and/or *ex situ* germplasm collections in Brazil.

Materials and methods

Population sites, collection of samples and DNA extraction

Adult trees of *Swietenia macrophylla* were sampled from seven natural populations near the southern boundary of the Brazilian Amazon. Sample sites were located at distances between 8 and 2103 km apart (Fig. 1). Populations were selected on the basis of accessibility and to maximize regional representation for the species. Leaf samples were collected from 24 to 34 individuals per population. Sample sizes varied among populations because of the relative ease with which individualized tree crowns could be reached. The leaves were dried in silica gel, and stored at −20 °C until DNA extraction. Total genomic DNA was extracted from the leaves following a standard CTAB procedure (Doyle & Doyle 1987). DNA quantification was performed by comparison with known concentrations of a DNA standard (Lambda DNA) in ethidium bromide-stained 1% agarose gels.

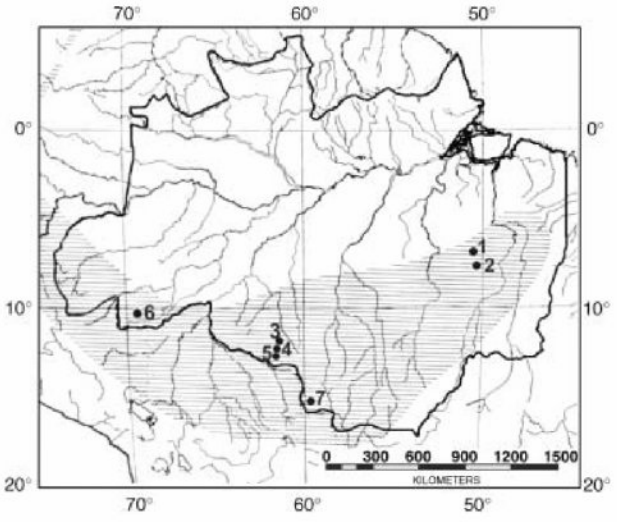

Fig. 1 Geographical distribution of *Swietenia macrophylla* in the Brazilian Amazon (dashed lines) and localization of the seven populations sampled: (1) A. Azul; (2) Maraj; (3) P. Bueno; (4) Cach. A; (5) Cach. E; (6) C. Mendes and (7) P. Lacerda.

Microsatellite analysis

Microsatellite marker analysis of 194 individuals representing the seven populations was carried forward using eight marker loci developed and optimized for *S. macrophylla* (Lemes *et al.* 2002). Microsatellite locus amplifications, electrophoresis conditions and allele-size determinations by fluorescence detection in multiplexed assays were carried out as described by Lemes *et al.* (2002). To avoid incomplete + A addition, minimize stutter peaks, and allow the multiplexing of several loci in the same polymerase chain reaction (PCR), a hot start PCR procedure and a final elongation step at 72 °C for 45 min were used.

Data analysis

To estimate overall levels of genetic diversity, the following measures were calculated for all populations using the GDA software (Lewis & Zaykin 1999): mean number of alleles per locus (A), and mean observed (H_O) and mean expected (H_E) heterozygosity. Tests for departure from Hardy–Weinberg equilibrium were performed using the *U*-test (Raymond & Rousset 1998) considering the hypotheses of heterozygote deficiency and excess, using GENEPOP 3.1.c (Raymond & Rousset 1998). Exact *P*-values were determined by a Markov chain method (Guo & Thompson 1992) implemented in GENEPOP 3.1.c (Raymond & Rousset 1998).

The extent and significance of the genetic differentiation among populations was investigated by estimating the fixation indices based on two models: (i) the infinite allele model (Kimura & Crow 1964) and (ii) the stepwise-mutation model (Ohta & Kimura 1973). Unbiased estimates of Wright *F*-statistics (Weir & Cockerham 1984) were obtained under the infinite allele model using FSTAT version 2.9.1 (Goudet 2000). We estimated θ, an estimator of Wright's fixation index F_{ST}, over all populations and for each pairwise population comparison; *f*, the within-population inbreeding, which measures the correlation of allele frequencies among individuals within populations; and *F* the overall inbreeding that measures the correlation of allele frequencies within individuals in different populations (Cockerham 1969). The statistical significance of θ, *f* and *F* were tested by bootstrapping over loci with a 95% nominal confidence interval (Goudet 2000). Significance tests of multilocus pairwise θ were carried out using the software FSTAT version 2.9.1 (Goudet 2000) with Bonferroni corrections. Genetic differentiation under the stepwise-mutation model was assessed by ρ, an estimator of Slatkin's R_{ST} (Slatkin 1995) and analogous to F_{ST}. The estimate of ρ was obtained by calculating the between- and within-population components of variance of allele sizes for all loci, populations and pairwise population comparisons using the software R_{ST} CALC, version 2.2 (Goodman 1997). Significance levels were determined after 1000 bootstraps with 95% nominal confidence intervals. Permutation tests (Lynch & Crease 1990) were carried out to determine if observed values of ρ were significantly different from zero.

Finally, the hypothesis that populations are differentiated because of the isolation-by-distance (Wright 1943) was tested by correlating pairwise θ and ρ against the pairwise geographical distance. The Spearman Rank correlation coefficient was calculated and significance was determined with 1000 permutations using the Mantel procedure (Mantel 1967). The Mantel test was carried out using the software GENEPOP version 3.1.c (Raymond & Rousset 1998).

Results

Genetic diversity and Hardy–Weinberg equilibrium

All microsatellite loci surveyed were highly polymorphic. The mean number of alleles per locus was 18.4 (range 13–27) (Table 1), whereas the mean number of alleles observed per locus per population was 9.5 (range 7.6–10.7) (Table 2). The mean expected heterozygosity (H_E) was generally higher than the mean observed heterozygosity (H_O), with only one locus showing the same value for both estimates (Table 2). Of the 56 tests of conformity to Hardy–Weinberg proportions, seven showed a significant departure from expected proportions at the 5% level. Based on the estimates of the inbreeding coefficient (*f*) all significant deviations were due to a deficit of heterozygotes (Table 2).

Population differentiation, structuring and isolation by distance

Over all loci and populations, the mean coefficient of inbreeding (*f*) was low but significantly different from

Table 1 Characterization of eight microsatellite loci, pooling individuals from seven populations of *Swietenia macrophylla* in the Brazilian Amazon

Locus	*N*	A	H_E (range)	H_O (range)
sm01	190	18	0.847 (0.222–0.904)	0.679 (0.235–0.920)
sm22	189	17	0.830 (0.525–0.837)	0.698 (0.500–0.823)
sm31	192	27	0.926 (0.807–0.922)	0.833 (0.783–0.967)
sm32	193	17	0.913 (0.774–0.900)	0.767 (0.559–0.880)
sm40	188	13	0.763 (0.629–0.769)	0.734 (0.592–0.840)
sm46	193	17	0.885 (0.790–0.901)	0.824 (0.760–0.875)
sm47	194	17	0.799 (0.379–0.836)	0.696 (0.360–0.853)
sm51	190	21	0.845 (0.715–0.903)	0.763 (0.500–0.909)
Mean over all loci		18.4	0.851	0.749

The SSR locus name; *N*, number of individuals; A, total number of alleles; H_E, expected heterozygosity; H_O, observed heterozygosity. H_E and H_O range estimated across populations.

Table 2 Microsatellite diversity in seven populations of *Swietenia macrophylla* in the Brazilian Amazon averaged over loci

Population	N	A	H_E	H_O	f
A. Azul	29.4	8.4	0.761	0.753	0.012
Cach. A	32.0	10.7	0.785	0.781	0.005
Maraj	25.0	9.2	0.793	0.740	0.068**
P. Lacerda	23.3	9.7	0.812	0.812	−0.004
C. Mendes	34.0	10.6	0.754	0.709	0.060***
Cach. E	24.0	10.2	0.810	0.780	0.042*
P. Bueno	23.5	7.6	0.754	0.680	0.100**
Over all populations	27.3	9.5	0.781	0.750	0.038***

N, mean sample size per locus; A, mean number of alleles per locus; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity, and within population coefficient of inbreeding (f).
Significant departures from Hardy–Weinberg expectations at *$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$.

Table 3 Single locus and overall locus estimates of Wright's F-statistics and genetic differentiation for the seven populations of *Swietenia macrophylla* in the Brazilian Amazon

Locus	f	F	θ	ρ
sm01	0.015	0.226	0.214	0.191
sm22	0.073	0.174	0.109	0.089
sm31	0.072	0.106	0.037	0.139
sm32	0.095	0.166	0.079	0.195
sm40	−0.039	0.051	0.087	0.146
sm46	0.019	0.071	0.053	0.084
sm47	−0.008	0.150	0.157	0.145
sm51	0.055	0.105	0.053	0.190
Over all loci	0.038*	0.132*	0.097*	0.147*
Upper bound**	0.065	0.169	0.140	0.192
Lower bound	0.007	0.095	0.062	0.136

*$P < 0.0001$.
f, inbreeding coefficient; F, over all inbreeding coefficient, θ; fixation index; ρ; population differentiation based on the step-wise mutation model.
**95% confidence interval bounds on the estimates over all loci.

zero ($f = 0.038$, $P < 0.0001$). Four populations exhibited a significantly positive inbreeding coefficient, suggesting nonrandom mating of individuals within these populations (Table 2). The value of F, the measure of inbreeding that considers both the effects of nonrandom mating within and among populations, was significantly different from zero ($F = 0.132$, $P < 0.0001$), giving evidence of population structure (Table 3).

The two overall measures of population differentiation θ and ρ were both significantly greater than zero (θ = 0.097 and ρ = 0.147, $P < 0.0001$), indicating a moderate but significant degree of genetic differentiation among populations of *Swietenia macrophylla* in the Brazilian Amazon (Table 3). The estimates of ρ were numerically greater than the estimates of θ for 15 out of the 21 pairwise population comparisons (Table 4).

Table 4 Pairwise multilocus estimates of genetic differentiation, θ and ρ, among seven populations of *Swietenia macrophylla* in the Brazilian Amazon

Population comparison	Distance (km)	θ*	ρ**
Cach. A–Cach. E	8	0.130	0.135
Cach. A–P. Bueno	17	0.046	0.129
Cach. E–P. Bueno	24	0.122	0.087
A. Azul–Maraj	107	0.034	0.036
P. Lacerda–Cach. E	375	0.082	0.074
Cach. A–P. Lacerda	381	0.095	0.053
P. Lacerda–P. Bueno	389	0.103	0.106
Cach. A–C. Mendes	882	0.156	0.207
C. Mendes–Cach. E	884	0.087	0.079
C. Mendes–P. Bueno	884	0.144	0.078
P. Lacerda–C. Mendes	1216	0.085	0.117
Maraj–P. Lacerda	1258	0.052	0.169
A. Azul–P. Lacerda	1307	0.086	0.148
Maraj–P. Bueno	1323	0.071	0.160
Cach. A–Maraj	1334	0.076	0.160
Maraj–Cach. E	1337	0.081	0.096
A. Azul–P. Bueno	1342	0.066	0.139
A. Azul–Cach. A	1355	0.089	0.133
A. Azul–Cach. E	1358	0.114	0.097
Maraj–C. Mendes	2101	0.115	0.180
A. Azul–C. Mendes	2103	0.126	0.223

*For all pairwise comparisons of θ, nonadjusted P-values, $P < 0.0001$. For corrected P-values using standard Bonferroni procedure, $P < 0.005$. P-values obtained after 21000 permutations.
**For all pairwise comparisons of ρ, $P < 0.0001$, except for pair A. Azul × Maraj, where $P < 0.01$.

The correlation between ρ and the geographical distance for the 21 pairwise comparisons among the seven populations (Fig. 2) was positive and significant ($r = 0.617$; $P = 0.022$), suggesting a pattern of isolation by distance among the *S. macrophylla* populations in the Brazilian Amazon. No significant correlation with geographical distance was demonstrated based on pairwise θ-values ($P = 0.396$).

Discussion

Genetic diversity of Swietenia macrophylla *in the Brazilian Amazon*

Mahogany in South America is typically found in aggregations of several tens to hundreds of mature trees along seasonal streambeds and densities within aggregations may vary between 0.1 and 3 mature trees/ha (Grogan 2001;

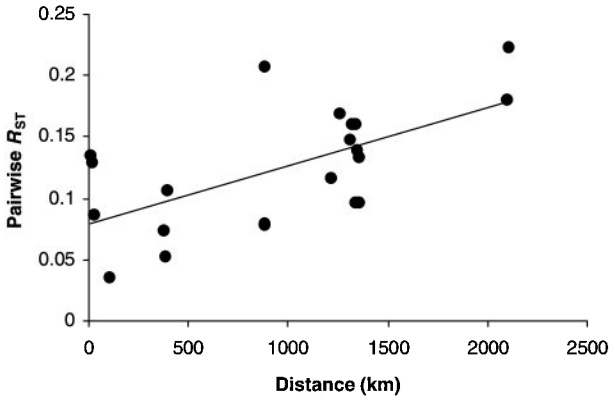

Fig. 2 Relationship between pairwise R_{ST} and geographical distance among populations of *Swietenia macrophylla* in the Brazilian Amazon (Mantel test of correlation, $r = 0.617$, $P = 0.022$).

Verissimo *et al.* 1995; Gullison *et al.* 1996). The aggregations are scattered in the forest matrix, so that there may be tens of kilometres separating the aggregations. Our sampling of around 30 adult trees per population (aggregation) therefore is likely to be a representative subsample of the genetic variability occurring in these restricted populations. The high levels of genetic diversity observed for *S. macrophylla* follow the pattern found in other microsatellite studies of tropical tree species (Aldrich *et al.* 1998; Dayanandan *et al.* 1999; White *et al.* 1999; Collevatti *et al.* 2001). It is noteworthy that the levels of genetic diversity (A, the mean number of alleles per locus; and H_E, the average gene diversity) for *S. macrophylla* in Brazil (A = 18.4 and $H_E = 0.78$) were higher than those found for the conspecific Central America populations (A = 13.0 and $H_E = 0.66$, Novick *et al.* 2003) analysed with seven out of the eight loci used in this study. It suggests that the more continuous forests in the Brazilian Amazon, where topographic barriers to gene flow seem to be minimal and there were more stable climatic conditions in South America during the Pleistocene (Whitmore & Prance 1987), may enhance the maintenance of the diversity. As expected for microsatellite loci with high mutation rates, the genetic diversity measures for *S. macrophylla* are high when compared to those derived from other kinds of markers such as isozymes (Loveless 1992).

At least two explanations may account for the deficit of heterozygotes observed in four populations. One possible explanation is the occurrence of null alleles, which fail to amplify because of mutations in the flanking primer sequences (Callen *et al.* 1993). Some studies have documented null alleles at microsatellite loci at frequencies of up to 15% (Callen *et al.* 1993; Paetkau & Strobeck 1995; Pemberton *et al.* 1995; Jarne & Lagoda 1996). However, this seems to be an unlikely explanation because amplification failures that would reflect null/null homozygotes were rare at all loci in the present study (maximum failure of 3% at locus sm40; Table 1). Furthermore stronger evidence for the absence of null alleles was also seen for these microsatellites in a mating system study we carried out in the Marajoara population (Lemes 2000). In that study, the allelic transmission from 25 mother trees to 400 progeny individuals was analysed for these same eight loci, and all offspring displayed at least one maternal allele.

The second explanation, which we favour in the case of Amazon mahogany, is that assortative mating, caused by spatial clustering or coincidence in flowering time among related groups of trees, has led to inbreeding and homozygote excess. The Marajoara mating system study (Lemes 2000) showed that *S. macrophylla* is predominantly outcrossed, but that some trees exhibit a considerable degree of selfing. Nonetheless, selfing is generally averted in mahogany because anthesis of male and female flowers is not usually synchronous within a tree (Styles 1972).

Genetic differentiation of S. macrophylla *in the Brazilian Amazon*

Both multilocus estimates of genetic differentiation, $\theta = 0.097$ and $\rho = 0.147$ indicate a moderate but significant degree of differentiation among populations of *S. macrophylla* in the Brazilian Amazon. Theory suggests that population differentiation is more accurately estimated by R_{ST}, because this measure better accounts for the high mutation rate of microsatellite markers (Hedrick 1999). In contrast, F_{ST} often underestimates population differentiation at microsatellite loci. Despite the high mutation rate of microsatellite loci, the value of θ (0.097) obtained for *S. macrophylla* is similar to the mean G_{ST} (0.11) value found for 37 different tropical taxa based on isozymes (Loveless 1992). However, the significance of the similarity in θ and G_{ST} is hard to assess given the differences in geographical scale, species life history traits and genetic markers among studies.

Relatively few studies have assessed genetic variation in natural populations of tropical tree species using microsatellites (Chase *et al.* 1996; Aldrich *et al.* 1998; Dayanandan *et al.* 1999; White *et al.* 1999; Collevatti *et al.* 2001). Two additional species in the same family as mahogany (Meliaceae) have been studied with microsatellites, *Carapa guianensis* in Costa Rica (Dayanandan *et al.* 1999), and *Swietenia humilis* in Honduras (White *et al.* 1999). Both species exhibited much lower levels of genetic differentiation ($\rho = 0.041$ and 0.032, respectively) among populations than found here for *S. macrophylla*. The spatial scale of the *C. guianensis* and *S. humilis* studies, with a maximum distance between populations of 44 km, stands in contrast to the 2100 km geographical scale of *S. macrophylla* examined here. Nonetheless, high levels of genetic differentiation were also observed between Amazonian populations Cach. A–Cach. E or Cach. A–P. Bueno, less than 20 km apart (Table 4).

Considering all Brazilian mahogany populations, the genetic distance measured by R_{ST} is significantly correlated with geographical distance, whereas pairwise estimates based on θ were not. Despite the debate on the accuracy of measures based on variance in allele frequencies under the infinite allele model vs. allele size under the stepwise mutation model, theoretical studies suggest that the latter seems to be more appropriate for quantifying levels of genetic differentiation with microsatellites (Valdes *et al.* 1993; Slatkin 1995; Goldstein & Pollock 1997).

Genetic differentiation among Amazonian mahogany populations probably reflects the interplay of ecological, evolutionary and biogeographic factors, such as pollen and seed dispersal mechanisms, demographic history and geographical barriers to gene flow (Alvarez-Buylla *et al.* 1996). Considering the large geographical scale of this study, our data indicate lower than expected levels of differentiation among Amazonian populations of *S. macrophylla*, given that it is a patchily distributed forest tree species that is pollinated by nonspecialist insects and whose seeds are dispersed by wind.

Factors that should limit gene flow in mahogany are the following. First, short-distance pollination is thought to generally restrict opportunities for gene exchange between populations. The minute flowers of mahogany are pollinated by a diverse array of generalist insects, such as small bees and moths (Styles 1972), which have limited foraging ranges compared with other more specialized vectors, such as bats, large or medium-sized euglossine bees (Frankie *et al.* 1976; Bawa 1990), or the small wind-dispersed wasps that pollinate fig trees (Nason & Hamrick 1997). Second, wind dispersal of seeds correlates with higher levels of genetic differentiation (Loveless 1992). While most tropical trees have animal-dispersed seeds, in mahogany, median wind seed-dispersal distances are only 32–36 m (Gullison *et al.* 1996).

Notwithstanding predictions of restricted gene flow based on mahogany life history traits, recent data on *Swietenia humilis* in a fragmented forest mosaic in Honduras have shown pollen movement at distances > 4.5 km (White *et al.* 2002). Such long-distance pollination promoted by nonspecialist insects may be one factor behind the relatively weak population genetic structure of Amazonian mahogany. In addition, the distance travelled by wind-dispersed seeds may be underestimated by current methods, particularly in light of the high frequency of storms and blow-downs in the Amazon (Nelson *et al.* 1994).

Our results suggest that landscape topography may play a role at least as important as life history in establishing the population structure of Brazilian mahogany. Pairwise population comparisons indicated low levels of genetic differentiation (ρ = 0.04) between the easternmost populations sampled (Marajoara and A. Azul), which are 107 km apart but located in a flat region with no notable geographical barrier between them. In contrast, populations from the Serra dos Parecis mountains (Cach. A, Cach. E and P. Bueno), exhibited considerably higher pairwise differentiation (ρ = 0.09–0.13) despite the short distance (8–24 km) between them. The pairwise ρ estimates between the Serra dos Parecis populations are only slightly lower than those found between eastern (Marajoara and A. Azul) and western populations (P. Bueno, Cach. A, Cach. E and C. Mendes) of mahogany, which lie 1323–2103 km apart and are separated by the Tapajos and Xingu rivers.

The modest pairwise divergence between western vs. eastern populations of mahogany suggests that major Amazonian rivers have not effectively isolated populations on either side, perhaps owing to headwater gene exchange or interfluvial gene flow during the drier and colder periods of the Pleistocene in the Amazon, when the large tributaries were probably much narrower (Maslin & Burns 2000). It is possible also that most populations share fairly recent ancestry as a result of recolonization of the current range from restricted glacial refugia. Our data suggest that mountains may represent a much more effective physical barrier to gene flow among *S. macrophylla* populations than the major Amazonian rivers. This is in accordance with findings in Mesoamerica (Novick *et al.* 2003), where the Talamanca mountains have apparently acted as a genetic barrier separating the Pacific and Atlantic populations of *S. macrophylla*.

Implications for conservation

Mahogany is threatened throughout its range in South America as a result of over-exploitation and habitat destruction, which have clearly reduced local population sizes and led many populations to local extinction (Verissimo *et al.* 1995; Grogan 2001). The distribution of *S. macrophylla* along the southern boundary of the Brazilian Amazon coincides with areas of higher deforestation rates collectively referred to as the 'Arc of Deforestation' including the Brazilian states of Pará, Tocantins, northern Mato Grosso, Rondônia and Acre. Habitat degradation caused by selective logging and, most importantly, through conversion of forest into soybean plantations and cattle ranches with recurrent use of fire is likely to reduce the colonization of new sites, despite the ability of mahogany to regenerate in disturbed habitats (Snook 1996). Deforestation and forest degradation have been so intense in this vast region that the genetic diversity of many remnant populations may already be compromised by genetic drift and inbreeding. Even establishing reserves provides no safeguard for mahogany as illegal extractions of this hardwood have been reported from National Parks and Indian reserves in Brazil and other countries (Rodan *et al.* 1992; Grogan 2001).

Clearly, the long-term survival of mahogany requires immediate protection of representative populations across

the species' geographical range. Our documentation of population genetic structure of Brazilian mahogany coupled with demographic data (Verissimo *et al.* 1995; Grogan 2001) provides a blueprint for designing conservation and management policies to maintain the genetic diversity of this valuable timber species. The very high level of genetic variation found within all populations, and the low densities of adult trees, indicate that *in situ* conservation strategies should be designed to preserve large areas to minimize the loss of diversity due to genetic drift. The predominantly allogamous mating system of *S. macrophylla* (Lemes 2000) suggests that breeding populations are large and gene flow is extensive in mahogany species, thus reinforcing the need to protect large forest areas.

The isolation by distance observed among Amazonian mahogany populations suggests that *in situ* reserves should be distributed evenly across the species' range in order to conserve maximally the regional genotypic diversity. Since mahogany is predominantly allogamous and resilient to some level of habitat disturbance and fragmentation (Lemes 2000; White *et al.* 2002), we recommend that *in situ* reserves be linked by smaller, managed areas in private lands, extractive reserves, or Indian territories, where limited selective logging may be allowed. These areas can act as corridors and stepping-stones for gene flow, and would provide a metapopulation structure to the managed and preserved populations. Regions that are topographically complex, like Serra dos Parecis, may warrant a more detailed conservation strategy, since populations in these areas tend to exhibit higher genetic differentiation. The occurrence of such microgeographical differentiation emphasizes the importance of maintaining populations in their diverse habitats, especially in areas with mosaics of topography and soils. Furthermore, *in situ* genetic conservation initiatives for mahogany should be associated with community-based conservation strategies aiming to protect samples of the rich, seasonal forests of the south Amazon boundary.

If the rate of deforestation and mahogany logging in remnant populations continues at current rates, especially along the southern boundary of the Brazilian Amazon, *ex situ* conservation policies should be urgently implemented. As mahogany seed viability decays rapidly, conservation should involve germplasm preservation realized through planted trees. Seed collection strategies for the establishment of *ex situ* seed banks should follow the same principle suggested for *in situ* conservation: sampling of several open-pollinated progeny arrays from broadly spaced trees representing populations covering a wide geographical range and later maintaining the identity of those provenances in the *ex situ* collection. More intensive sampling will be required in regions of high topographic relief and heterogeneous soil types.

A number of studies in recent years have used high throughput DNA marker technologies to describe the genetic diversity of Neotropical tree species at increasingly larger geographical scales and finer population structure (e.g. Chase *et al.* 1996; Aldrich *et al.* 1998; Dayanandan *et al.* 1999; White *et al.* 1999; Collevatti *et al.* 2001; White *et al.* 2002). Although such studies have contributed significantly to the understanding of the general patterns of genetic variation and dynamics of tropical trees, efforts to translate such knowledge into effective conservation practices have been timid. By showing that populations of Brazilian Amazon mahogany are isolated by distance and by regional topography, this study attempts to provide the basis for sound *in situ* and *ex situ* conservation planning. It should be kept in mind, however, that conservation of tropical trees involves not only theoretical considerations based on the genetics of the species, but also complex social and economical issues.

Acknowledgements

The study was funded by the Brazilian Ministry of Science and Technology (CNPq/PADCT grant no.62.00059/97-4 to D.G., CNPq/RHAE fellowship no. 260021/94.6 to M.R.L.), World Wildlife Fund — Brazil (Program Natureza e Sociedade, grant no. CSR 95–033 to M.R.L.), and Fundação Botânica Margareth Mee, whom we gratefully acknowledge. We also acknowledge partial financial support for this study from the European Commission, DGXII, International Cooperation with Developing Countries Programme contract number ERBIC18CT970149, and the Pilot Program to Protect the Brazilian Rain Forests (PPG-7, European Union and Brazilian Ministry of Science and Technology). Thanks to José Ribeiro, Jimmy Grogan, Jurandir Reis Galvão, Orlandino Candiotto and Jerônimo M. de Souza for their kind assistance during field work. Our thanks to Jaime Tadeu França (IBAMA) for his help in arranging plant collections in many areas and Rosana P. V. Brondani for technical and laboratory support. We are grateful to Eldredge Bermingham and Chris Dick for valuable comments on the manuscript. We also acknowledge the support of IBAMA (Brazilian Ministry of Environment) and EMBRAPA (Brazilian Ministry for Agriculture).

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