High levels of pollen dispersal detected through paternity analysis from a continuous Symphonia globulifera population in the Brazilian Amazon

Francimary da Silva Carneiro, Bernd Degen, Milton Kanashiro, Andre Eduardo Biscaia de Lacerda, Alexandre Magno Sebbenn

1. Introduction

In recent years, tropical forests have experienced high rates of deforestation through processes of clear cutting and logging which have reduced many large continuous forests to isolated patches in highly fragmented landscapes (Sebbenn et al., 2008). The process of land conversion from forest to agriculture has turned continuous tree populations into small isolated ones, while selective logging has reduced the effective population size of continuous populations by harvesting the largest and reproductively active trees. The fragmentation of populations and the removal of large numbers of the reproductive population may affect the viability of many tree species populations, especially in the species-rich Amazon tropical forest. In the Amazon, more than 100 different tree species might be found in a single hectare with most species occurring in very low-densities, typically with less than 1 tree/ha (Dick et al., 2003a; Azevedo et al., 2007; Carneiro et al., 2007; Cloutier et al., 2007; Lemes et al., 2007; Lacerda et al., 2008; Silva et al., 2008). Fragmentation and selective logging can therefore affect the mating system of a species by increasing the distance between conspecifics.

Studies have shown, however, that many low-density tropical species have a generally high outcrossing rate, i.e. >0.8 (Ward et al., 2005), suggesting that most of the pollen dispersal occurs over long distances. These high outcrossing values can be partially the result of inbreeding depression which eliminates selfed-seeds from progeny arrays (Gribel and Gibbs, 2002; Hufford and Hamrick, 2003; Naito et al., 2005; Del Castillo and Trujillo, 2007). Long distance pollen dispersal has been reported for many low-density animal pollinated tropical trees in both natural and fragmented stands (Dawson et al., 1997; White et al., 2002; Dick et al., 2003a; Kenta et al., 2004; Latouche-Hallé et al., 2004; Lacerda et al., 2008; Lourmas et al., 2007; Silva et al., 2008). Thus, it is possible that some of these tropical tree species could be resilient to various levels of spatial isolation caused by anthropogenic factors, at both the individual and population levels.

Both pollen and seed dispersal are factors which influence the gene flow of a population. Gene flow, in turn, determines the genetic diversity both within a population and among different generations of a population (Dow and Ashley, 1998). Understanding the extent to
which both pollen and seed dispersal influence gene flow is essential in examining the potential of a species to adapt quickly to environmental and land use changes and it is also imperative in the creation and implementation of appropriate strategies for conservation (Dawson et al., 1997; Odduo-Muratorio et al., 2005; Larsen and Kjaer, 2008), logging (Kanashiro et al., 2002), and seed collection for reforestation purposes (Bittencourt and Sebbenn, 2007).

Successful pollen dispersal can be directly studied in tree populations using microsatellite loci, paternity analysis, and progeny arrays, preferably from known seed-trees (in this study seed-trees are defined as the individual tree which provided the seed for germination and genetic study). Microsatellite loci, due to their typically high polymorphism in terms of the number of low-frequency alleles, generally present a high exclusion probability (>0.99) and are therefore an ideal marker for paternity analysis studies (Dawson et al., 1997; Dow and Ashley, 1998; Smouse and Sork, 2004). Microsatellite paternity analysis assumes that there are no mutations between parents and offspring and that adults and offsprings with matching genotypes are related (Dow and Ashley, 1998). In order to study contemporary pollen flow, a well defined area is required in which the seed-trees and putative pollen donors are genotyped using microsatellite markers and the spatial position of each individual is known (Smouse and Sork, 2004). The optimal study area can be a small forest fragment or a plot established inside a continuous forest. For low-density tree populations (<1 tree/ha) in a continuous forest, the plot must be sufficiently large to ensure a substantial number of trees for which the paternity of the seeds can be tested (for example, at least 100 putative pollen donors and therefore an area of more than 100 ha). Thus, with a sufficient number of microsatellite loci evaluated in progeny arrays and collected within a well defined population or plot, pollen gene flow can be estimated. This estimate considers the percentage of pollen donors for which all trees in the plot are excluded as possible fathers of the seeds. From this, pollen dispersal distance can be traced by analyzing the relative locations of the seed-trees and the potential pollen donors (Dow and Ashley, 1998; Burczyk et al., 2004; Smouse and Sork, 2004).

In the present study, pollen gene flow was investigated over two consecutive years in a continuous forest Symphonia globulifera population, located within an experimental plot in Tapajós National Forest, Brazil. In a previous study within the same plot, S. globulifera's mating system was shown to occur only by outcrossing with a small proportion of mating occurring among relatives (Carneiro et al., 2007). Carneiro et al.'s (2007) study used an indirect method (TWOGENER analysis) to determine pollen dispersal distance which was estimated between 144 and 444 m. In our study, a direct method of pollen dispersal is used based on paternity analysis and six microsatellite loci in S. globulifera. This study seeks to address the following questions: (i) what is the proportion of pollen immigration from outside of the plot? (ii) Considering the low-density of reproductive trees in the study site, what is the average distance of pollen dispersal? (iii) Is the pollen dispersal within the plot a function of the spatial distance between seed-trees and potential pollen donors?

2. Materials and methods

2.1. Study species

S. globulifera L. F. (Clusiaceae) is a hermaphroditic animal pollinated tropical tree species with a wide natural distribution. S. globulifera occurs in the neotropics, from Mexico to Rio de Janeiro State (South-eastern Brazil), and is also found in tropical West Africa (Dick et al., 2003b). In the Amazon forest, the species is a medium sized tree, reaching up to 40 m in height and more than 90 cm in diameter at breast height (dbh). In the Central Amazon, hummingbirds are the principal pollinators (Bittrich and Amaral, 1996; Maues, 2001) and the density of the population is less than 1 tree/ha (Carneiro et al., 2007).

2.2. Site and the sample size

The study population is situated in a 500 ha experimental plot in the Tapajós National Forest (TNF) south of Santarém, Pará State, Brazil (2°51'S and 54°57'W and 175 m above sea level) (Fig. 1). The plot is located on a flat plateau which is covered by a dense terra firme forest and the area is not influenced by seasonal river flooding. The climate is tropical with a mean annual rainfall of 2000 mm (concentrated from February to May) and a dry season of two to three months (August–October) with annual temperatures averaging at 25 °C. The experimental plot was established by the Endoregene Project (Embrapa Amazônia Oriental/DFID) as an Intensive Study Plot for Ecological and Genetic Studies (Kanashiro et al., 2002).

The 500 ha plot was subdivided into six subplots: four 100 ha subplots (subplots 3–6) and two 50 ha subplots each (subplots 1 and 2) (Fig. 1). Within each subplot, all S. globulifera trees with a diameter at breast height (dbh) of 20 cm or greater were identified and mapped, resulting in a density of 0.332 tree/ha. The distance among trees in all subplots ranged from 14 to 2962 m, with an average of 1234 m.

Data collection for this study included cambium samples from 90% of all mapped trees (161 sampled out of a total of 179 trees). Seeds were collected from 26 seed-trees in 2002 and from 30 seed-trees in 2003 (Fig. 1). In order to ensure accuracy in seed sampling, collection of seeds was conducted directly in the tree's canopy. Seeds from the same trees were collected in both years from 19 individuals because not all seed-trees sampled in 2002 produced seeds in 2003. Seeds were germinated as a single tree's progeny. Microsatellites were amplified for 261 seeds from 2002 (7–15 seeds per tree) and 487 seeds from 2003 (12–30 seeds per tree). The distance between sampled seed–trees varied between 26 and 2951 m with a mean of 1282 m in 2002 and 1295 m in 2003. The
using the allele frequencies of the adult population as reference.

Ex

heterozygosity (\(D\)) was estimated using the program CERVUS 3.0

\(\hat{D}\) was calculated as

\[ \hat{D} = 1 - \left( \frac{H_o}{H_e} \right) \]

The statistical significance of \(F\) for each locus and average loci was tested using permutation. All cited indexes and permutations were calculated using the FSTAT program (Goudet, 1995). The paternity exclusion of the second parent was determined by the maximum-likelihood assignment (Meagher, 1986) using the CERVUS 3.0 program (Marshall et al., 1998; Kalinowski et al., 2007). We also tested the hypotheses that center seed-trees received 90% of the pollen from trees located within the plot and 10% from outside the plot, and outer seed-trees received 50% of the pollen from trees located within and 50% from outside the plot, using a log-likelihood G test (Sokal and Rohlf, 1981).

### 3. Results

#### 3.1. Genetic diversity and fixation index

A high level of polymorphism and genetic diversity were detected in the loci used in this study. Nineteen to 29 alleles were detected among loci in the total sample (759 individuals), resulting in 146 alleles and an average of all loci of 24.4. Among the sampled population, 144 alleles were detected in adult trees (Table 1), 133 in seeds from 2002, and 136 in seeds from 2003. Of all adult trees (Table 1), the observed heterozygosity was high and ranged from 0.728 to 0.866, with an average of 0.783. The expected heterozygosity was higher than the observed heterozygosity.

#### Table 1

<table>
<thead>
<tr>
<th>Locus</th>
<th>(k)</th>
<th>(H_o)</th>
<th>(H_e)</th>
<th>(F)</th>
<th>(P_{Excl(2)})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sg03</td>
<td>21</td>
<td>0.857</td>
<td>0.883</td>
<td>0.020</td>
<td>0.239</td>
</tr>
<tr>
<td>Sg18</td>
<td>19</td>
<td>0.866</td>
<td>0.888</td>
<td>0.025</td>
<td>0.228</td>
</tr>
<tr>
<td>Sg06</td>
<td>29</td>
<td>0.762</td>
<td>0.932</td>
<td>0.182*</td>
<td>0.140</td>
</tr>
<tr>
<td>Sg08</td>
<td>24</td>
<td>0.744</td>
<td>0.891</td>
<td>0.164*</td>
<td>0.211</td>
</tr>
<tr>
<td>Sg09</td>
<td>24</td>
<td>0.740</td>
<td>0.925</td>
<td>0.200*</td>
<td>0.157</td>
</tr>
<tr>
<td>Sg10</td>
<td>29</td>
<td>0.728</td>
<td>0.925</td>
<td>0.213*</td>
<td>0.152</td>
</tr>
<tr>
<td>Means</td>
<td>24</td>
<td>0.783</td>
<td>0.907</td>
<td>0.137*</td>
<td>0.001</td>
</tr>
<tr>
<td>All locus</td>
<td>144</td>
<td>0.9996</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For each loci: observed number of alleles (\(k\)); observed heterozygosity (\(H_o\)); expected heterozygosity (\(H_e\)); fixation index (\(F\)); second parent exclusion probability (\(P_{Excl(2)}\)).

\* \(P < 0.01\)
(ranging from 0.883 to 0.932, with an average 0.907), suggesting heterozygosity deficiency in relation to the Hardy–Weinberg principle. The fixation index ranged from 0.025 to 0.213, with an average of 0.137. The fixation index was statistically significantly different for four loci among the six analyzed as well as for the average of all loci \( (P < 0.01) \).

### 3.2. Paternity analysis

The paternity exclusion probability of the second parent for six loci was very high in this study \( (0.99996; \text{Table 1}) \). Thus, the probability of cryptic gene flow (foreign gametes with multi-locus genotypes that can also be generated by local males) was very low, resulting in 0.0064 \( (1 \text{ locus genotypes that can also be generated by local males}) \) was probability of cryptic gene flow (foreign gametes with multi-locus genotypes that can also be generated by local males) was very low, resulting in 0.0064 \( (1 \text{ locus genotypes that can also be generated by local males}) \) was probability of cryptic gene flow (foreign gametes with multi-locus genotypes that can also be generated by local males) was very low, resulting in 0.0064. In testing the hypotheses regarding location of pollen donors the results showed a statistically significant difference for the center area, father assignment rates were 54% in 2002 and 53% in 2003. At the outer area in 2002 and 2003. A low number of self-sibs was found for both years and the average selfing rate was estimated at 1.9% in 2002 and 2.6% in 2003. Excluding selfing, father assignment was higher for seed-trees located in the center of the plot than seed-trees near the edges. In the central area of the plot, father assignment rates were 88% in 2002 and 63% in 2003. At the outer area, father assignment rates were 54% in 2002 and 53% in 2003. In testing the hypotheses regarding location of pollen donors the results showed a statistically significant difference for the center seed-trees (90% within, 10% outside the plot) only in 2002 \( (G = 86.9, P < 0.01) \). In this case, an alternative hypothesis was tested, assuming that 70% of the pollen was received from trees located within the plot and 30% from outside the plot. This hypothesis showed no statistical significance \( (G = 3.09, P > 0.05) \). No significant differences were observed for the hypothesis of outer seed-trees receiving 50% of the pollen from trees located within the plot and 50% from outside the plot in 2002 \( (G = 1.02, P > 0.05) \) and 2003 \( (G = 0.77, P > 0.05) \). Thus, the location of a seed-tree can affect the rate of pollen immigration. Of the 161 potential pollen donors, 66 (41%) sired at least one seed in 2002 (1–7 seeds), while in 2003, 82 (51%) donors sired at least one seed (1–16 seeds). Therefore, over the two-year study period 111 potential donors (69%) sired at least one seed.

### 3.3. Pollen dispersal distance

The results of the analysis showed that pollen dispersal occurs over long distances within the study area (Table 2, Fig. 3). Including selfing, the average distance of pollen dispersal \( (d) \) for seeds collected in 2002 was 880 m \( (\pm 660 \text{ m, SD}) \) and for seeds sampled in 2003 was 919 m \( (\pm 566 \text{ m, SD}) \). Excluding selfing, the distance of pollen dispersal measured for 2002 ranged from 46 to 2832 m \( (\bar{d} = 907 \pm 652 \text{ m}) \) and in 2003 from 26 to 2658 m \( (\bar{d} = 963 \pm 542 \text{ m}) \). In both years, there is a significant negative correlation between effective pollen dispersal and the distance between seed-trees and assigned pollen donors \( (r_{2002} = -0.93, P < 0.05; r_{2003} = -0.80, P < 0.05; r_{2002-2003} = -0.62, P < 0.05) \). This negative correlation suggests that mating tends to occur among trees which are closer

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**Table 2**

Profiles of pollen flow for grouped seed-trees located closer to the center (central) and closer to the edges (outer) of the plot for seeds collected in 2002 and 2003. Sample size \( n \); self-fertilization rate \( s \); pollen flow from within plot, pollen immigration; mean pollination distance within the plot \( (\pm \text{standard deviation}) \) in Symphonia globulifera.

<table>
<thead>
<tr>
<th>Sample</th>
<th>( n )</th>
<th>( s )</th>
<th>Pollen flow</th>
<th>Distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Within plot</td>
<td>Outside plot</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Including selfing</td>
<td>Excluding selfing</td>
</tr>
<tr>
<td>2002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central</td>
<td>64</td>
<td>0.016 (1)</td>
<td>0.88 (56)</td>
<td>0.13 (8)</td>
</tr>
<tr>
<td>Outer</td>
<td>142</td>
<td>0.021 (3)</td>
<td>0.54 (77)</td>
<td>0.46 (65)</td>
</tr>
<tr>
<td>Total</td>
<td>206</td>
<td>0.019 (4)</td>
<td>0.65 (133)</td>
<td>0.35 (73)</td>
</tr>
<tr>
<td>2003</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central</td>
<td>173</td>
<td>0.023 (4)</td>
<td>0.63 (109)</td>
<td>0.37 (64)</td>
</tr>
<tr>
<td>Outer</td>
<td>219</td>
<td>0.027 (6)</td>
<td>0.53 (116)</td>
<td>0.47 (103)</td>
</tr>
<tr>
<td>Total</td>
<td>392</td>
<td>0.026 (10)</td>
<td>0.57 (225)</td>
<td>0.43 (167)</td>
</tr>
</tbody>
</table>

Min/max: minimum and maximum distance of pollen dispersal, excluding selfing.

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**Fig. 3.** Frequency distribution of pollen-dispersal distance for seeds from 2002 (a), 2003 (b), 2002 and 2003 (c) and distance between reproductive trees and seed-trees (d) in a plot of Symphonia globulifera.
together. Our estimate of the correlation between dbh of possible pollen donors and the number of produced sibs was not statistically significant ($r = 0.11, P > 0.05$).

Excluding selfing, 50% of the pollen was dispersed up to 748 m in 2002 and up to 880 m in 2003 (median values). Considering each year individually and both years together, more than 90% of the pollen was dispersed up to 1000 m (Fig. 3). Significant differences between the frequency distribution of detected pollen dispersal distance and the frequency distribution of seed-trees and all other sampled trees in the plot was detected by the Kolmogorov–Smirnov test for seeds in the three situations: 2002 ($D = 0.236, P < 0.0001$), 2003 ($D = 0.132, P = 0.004$), and both years combined ($D = 0.147, P < 0.0001$; Fig. 3). These results indicate that the distance between potential male parents and seed-trees cannot explain the observed mating patterns. This test also shows that the frequency distribution of pollen dispersal distance in 2002 was significantly different from 2003 ($D = 0.256, P < 0.0001$). However, when this test was made only for the same seed-trees sample in both years, no difference was observed ($D = 0.134, P < 0.149$). Pollen dispersal distance was also estimated exclusively for seed-trees located closer to the edges (outer) of the plot and those closer to the center of the plot (central). Excluding selfing, the average pollen dispersal distance for central seed-trees was higher than outer seed-trees with outer at 791 ± 457 m in 2002 and 917 ± 437 m in 2003 and central at 994 ± 760 m in 2002 and 1006 ± 625 m in 2003 (Table 2).

4. Discussion

4.1. Outcrossing rate

Despite the low-density of reproductive trees in the studied S. globulifera population, the results of paternity analysis show the maintenance of very high outcrossing rates and, consequently, long pollen dispersal distances. Very low levels of selfing were also found in both reproductive events with a maximum of 2%. These results are similar to previous estimates of multilocus outcrossing rates carried out by Carneiro et al. (2007). Although the study conducted by Carneiro et al. (2007) used the same data set as this study, the mixed mating-model (Ritland and Jain, 1981) was used and resulted in outcrossing rates of 1.0 in 2002 and 0.998 in 2003. Elsewhere, self-fertilization rates have been reported by Aldrich and Hamrick (1998) for S. globulifera populations in continuous forests, fragmented forests and pastures in Costa Rica, with a minimum outcrossing rate of 0.731. Degen et al. (2004) also found some levels of self-fertilization and an outcrossing rate of 0.920 in a high-density S. globulifera population (>10.6 trees/ha) in French Guiana. The variations in outcrossing rates between sites suggest that the species is not self-incompatible and some self-fertilization does occur. Therefore, self-incompatible systems can be excluded as the possible cause of the observed high outcrossing rate in this study.

An alternative hypothesis is the inbreeding depression that occurs between the fertilization event and the moment of the seedlings’ microsatellite analysis. The inbreeding depression could eliminate part of the self-fertilized embryos, leaving only the genotypes of outcrossed seedlings accessible to markers, thus increasing the outcrossing rate estimate. In this case, the observed outcrossing rate is not the realized one, but the effective outcrossing rate. This phenomenon has been observed in various tropical tree species, such as Pseudobombax munguba (Mart. et Zucc.) Dugand (Gribel and Gibbs, 2002), Platyphyllum elegans Vog. (Hufford and Hamrick, 2003), Neobalanocarpus heimi (King) Ashton (Naito et al., 2005) and Pinus chiapensis (Mart) Andresen (Del Castillo and Trujillo, 2007).

4.2. Patterns of pollen dispersal

The cryptic gene flow estimate was very low (0.0064) in this study, indicating that it did not skew the estimates of pollen dispersal. Therefore, the seeds from both years that could not be assigned to any potential pollen donor within the plot are likely to represent pollen that originated from trees located outside the study area or from the 18 S. globulifera trees in the plot that were not genotyped.

Our results show extensive pollen movement in the study plot with a minimum pollen immigration of 35%. However, according to Kolmogorov–Smirnov test, patterns of effective pollen dispersal were not explained by distance between seed-trees and all other potential male parents within plot (Fig. 3). Pollen was predominantly dispersed in shorter distances than expected with 63% of the pollen travelling less than 1000 m. The maximum average pollen dispersal distance within the plot was 963 m (seeds from 2003; Table 2) which is shorter than the average distance between seed-trees and all other reproductive trees (1234 m), thus indicating a tendency toward pollination between trees which are closer together. This pattern is likely affected by the reproductive phenology of trees in the study area. During data collection we observed that not all reproductive trees in the plot produce flowers and fruits every year suggesting flowering of individuals may not be fully synchronised. Consequently, only approximately 50% of the trees within the plot fathered seeds in each year studied. Thus, flowering phenology limits the mating among reproductive trees and might explain the differences in pollen dispersal patterns which in this study are related to the occurrence of pollinization between trees that are closer together as well as the difference in pollinization distance between years.

The higher frequency of short-distance pollen dispersal is similar to that observed in other studies of pollen dispersal in various tree species. Similar results were reported for the tropical animal pollinated Dickorycia guianensis Amsh (Latouche-Hallé et al., 2004), Dipterocarpus tempehes Slooten (Kenta et al., 2004), Entandrophragma cylindricum (Sprague) Sprague (Sapeli) (Lourmas et al., 2007), Hymenaea courbaril L. (Lacerda et al., 2008), and Shorea acuminate Dyer (Naito et al., 2008). The distances of pollen dispersal detected from paternity analysis in this study were also higher than the results detected from previous studies. Carneiro et al.’s (2007) study using the same data set and Two GENER analysis (Smouse et al., 2001) reported pollen dispersal rates of 444 m in 2002 and 154 m in 2003. Similarly, a study from a high density S. globulifera population in Paracou, French Guiana showed dispersal rates ranging from 27 to 53 m (Degen et al., 2004). The difference in pollen dispersal between the Amazon forest population and Paracou is likely due to the differences in population density as the Amazon population has a low-density at 0.322 tree/ha, and Paracou a very high density at more than 10.6 trees/ha, as discussed by Carneiro et al. (2007). The lower estimates of pollen dispersal distance by Two GENER analysis, as reported by Carneiro et al. (2007), are the results of the type of analysis used in the study. Two GENER analysis is an indirect method of quantification of contemporary pollen dispersal and is based on assumptions about the shape of the pollen dispersal curve (normal, exponential, leptokurtic, etc.; Smouse and Sork, 2004). As a consequence, Two GENER analysis tends to underestimate average pollen dispersal distance due to an emphasis on effective pollen movement (Smouse and Sork, 2004). In contrast, the paternity analysis used in this study is a direct method which is not dependent on dispersal functions and is therefore a more accurate estimate of contemporary pollen dispersal.
4.3. Center versus outer seed-trees

The results confirmed our hypothesis that the location of the seed-trees can affect the rate of pollen immigration. Seed-trees located in the center of the plot had a significantly higher number of pollen donors detected inside of the plot than seed-trees located close to the edges of the plot. In addition, as hypothesized, the results showed that outer seed-trees received about 50% of the pollen from trees located within plot and 50% from outside. These results are significant and they suggest that studies of the patterns of pollen dispersal in plots established in continuous forest areas must consider the location of selected seed-trees in order to increase father assignment and to better estimate the frequency distribution of effective pollen dispersal.

Differences were also observed between years for the patterns of pollen dispersal (Fig. 3). Patterns and distance of pollen dispersal, as well as mating systems, can change between years as a result of changes in the flowering phenology, environmental changes affecting the behaviour of the pollinators, or anthropogenic processes such as forest logging and fragmentation. In this study, the seed-trees sampled in both years showed no difference in the patterns of pollen dispersal. The observed differences between years can be attributed to the variation of trees sampled in each year. However, differences between years in flowering phenology are common and studies of pollen gene flow must consider pollen dispersed from multiple reproductive events because a single pollen dispersal event may not represent the population pattern. Similar results were observed in *D. tempehes* (Kenta et al., 2004).

4.4. Implications for selective logging

*S. globulifera* is harvested in the Brazilian Amazon for timber production using selective logging practices (Carneiro et al., 2007; Sebbenn et al., 2008). The selective logging approach applied in Brazil is an adaptation of the reduced impact logging (RIL) system which may remove up to 90% of the largest trees (dbh > 50 cm) during a single harvesting episode. Trees with bad stem form, hollows or other apparent defects are not logged and are left as “seed-trees”, individuals designated to supply seeds for regeneration. This type of logging reduces the density of reproductive trees and increases the distance among reproductive conspecifics. Changes in reproductive population density caused by forest logging can affect a species’ mating system, by increasing self-fertilization and correlated mating levels (Lourmas et al., 2007). Such changes in mating systems have been detected in studies comparing outcrossing rates for trees located in continuous forests against rates from logged populations (Murawski et al., 1994; Obayashi et al., 2002; Ledig et al., 2005). Changes in outcrossing rates due to anthropogenic factors were also reported for *S. globulifera* (Aldrich and Hamrick, 1998). Their results suggest that anthropogenic processes increase the distance among conspecifics and reduce the density of reproductive populations which can affect the mating system of tree species.

The results of this study suggest that in an *S. globulifera* population located in a continuous, dense forest, the outcrossing rates are very high. Considering the results of Aldrich and Hamrick (1998), the reduction in population density and an increase in distance among conspecifics by logging could increase the self-fertilization rate in the population. However, *S. globulifera* is a middle-size low-density tree species in the Amazon and in our study area the dbh class distribution showed a positive skewed shape (Fig. 2). Therefore, logging up to 90% of trees with a dbh of ≥50 cm would reduce the reproductive population from 161 to 131 trees (18%) and would have a limited effect on the distance between reproductive trees, increasing it from 1234 m before logging to 1363 m after logging. However, the largest trees have also been described in some studies as the main contributors to pollination (Lattoche-Hallé et al., 2004; Lourmas et al., 2007). Changes in basal area of the population along with a reduction in the number of the largest trees could, therefore, affect the quantity of pollen dispersal. However, no association was found between dbh of possible pollen donors and the number of produced sibs. Thus, we do not expect that selective logging practices used in the Brazilian Amazon will substantially affect the mating system of the present population. These findings are in agreement with the results of Carneiro et al. (2007) which suggested that logging will not isolate the remaining trees in the study area.

Further studies modelling the effects of selective logging on tree populations also suggest the possible resilience of *S. globulifera* to fragmentation and isolation due to logging. Degen et al. (2006) and Sebbenn et al. (2008) have used Ecogene simulation analysis to study the long-term effects of selective logging practices on demographic structure and genetic diversity for four tropical tree species. Both studies observed that the *S. globulifera* species was unique in that it would likely be able to sustain the harvesting methods actually employed in French Guiana (logging intensity of 90%, minimum cutting dbh of 60 cm, and cutting cycles of 65 years) in the long term (six cutting cycles). This result can be explained by the small number of reproductive trees logged in each cutting cycle due to the high minimum cutting diameter. However, this hypothesis needs to be empirically confirmed through a study comparing the mating system and pollen dispersal before and after logging events.

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