Effects of Forest Fragmentation and Flowering Phenology on the Reproductive Success and Mating Patterns of the Tropical Dry Forest Tree *Pachira quinata*

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Abstract: The results of several studies suggest that forest fragmentation affects the mating patterns and reproductive success of tropical tree species by reducing pollinator activity, pollen deposition, and outcrossing levels. The flowering synchrony of trees has also been proposed as an additional factor in controlling fruit set and regulating levels of outcrossing, particularly in disturbed habitats. We examined the effects of forest fragmentation and flowering phenology on the reproductive success and genetic structure of the progeny produced by the tropical tree *Pachira quinata*. We conducted our study in the dry forest of Costa Rica and compared trees in two density and environmental conditions: (1) isolated trees separated by 500 m from other adult conspecifics and located in disturbed sites and (2) trees from continuous populations of groups of 20 or more reproductive individuals per hectare surrounded by undisturbed mature forest. Our study was conducted in the Guanacaste Conservation Area, Costa Rica, and surrounding areas. To evaluate flowering phenology, trees were classified as having synchronous or asynchronous flowering. The phenological stage of individuals was classified according to the proximity of the peak flowering date of each tree with respect to the mean peak flowering of the rest of the population. Six percent of the flowers produced a fruit in trees from continuous populations, whereas in isolated trees only 3% of the flowers did so. Fruit set was not affected by the flowering phenology of trees but was influenced mainly by factors associated with forest fragmentation. Seed production per fruit was not affected by forest fragmentation or flowering phenology. Overall, total fruit production per tree was not affected by forest fragmentation, because isolated trees tended to produce more flowers than trees from continuous populations. Genetic analysis revealed that the progeny of trees from continuous populations experienced lower levels of relatedness, a tendency for higher levels of outcrossing, and/or more sires than isolated trees. Our results suggest that forest fragmentation can have an effect on the mating patterns of *P. quinata*, reducing the number of outcross sires represented in the progeny of isolated trees.

Efectos de la Fragmentación de Bosques y la Fenología de Floración sobre el Éxito Reproductivo y los Patrones de Apareamiento de *Pachira quinata*, un Árbol de Bosque Tropical Seco

**Resumen:** Los resultados de varios estudios sugieren que la fragmentación de bosques afecta los patrones de apareamiento y el éxito reproductivo de especies de árboles tropicales al reducir la actividad de polinizadores, la deposición de polen y los niveles de exogamia. La sincronía de floración de árboles también ha sido propuesta como un factor adicional en el control de la producción de frutos y la regulación de niveles de exogamia, especialmente en hábitats perturbados. Examinamos los efectos de la fragmentación de bosques y la fenología floral sobre el éxito reproductivo y la estructura genética de la progenie producida por el árbol tropical *Pachira quinata*. Realizamos nuestro estudio en el bosque seco de Costa Rica y comparamos árboles en dos densidades y condiciones ambientales: (1) árboles aislados separados 500 m de otros adultos conspecíficos y localizados en sitios perturbados y (2) árboles en poblaciones continuas con grupos de 20 o

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Paper submitted March 21, 2002; revised manuscript accepted April 17, 2002.
more studies need to integrate genetic and reproductive information (Nason & Hamrick, 1997; Aldrich & Hamrick 1998; Cascante et al. 2002). This is of particular importance in plants with complex self-incompatibility systems and phenological patterns (Bawa 1974; Frankie et al. 1974; Hamrick & Murawski 1990).

In addition to the spatial isolation caused by forest fragmentation, temporal isolation caused by asynchronous flowering of individuals has been proposed as another important factor that affects the reproduction and genetic structure of plant populations in disturbed habitats (Murawski et al. 1990; Murawski & Hamrick 1991; Murawski & Hamrick 1992b; Chase et al. 1996; Doligez & Joly 1997; Nason & Hamrick 1997). Flowering phenology directly determines the effective number of pollen donors and the density of flowering individuals, both of which affect the patterns of pollen flow between trees (Stephenson 1982; Murawski & Hamrick 1992b). Trees that overlap in flowering period are likely to receive pollen from more pollen donors than trees with asynchronous flowering. In contrast, trees with asynchronous flowering may experience a reduction in reproductive output, with the number of pollen donors and the selfing rate being similar to those of trees found in isolated fragments. Therefore, the integration of flowering phenology data into forest fragmentation studies is required to understand variation in the reproductive success and genetic variability of fragmented populations (Murawski & Hamrick 1992b; Nason & Hamrick 1997).

We sought to determine the effects of flowering phenology and spatial isolation due to forest fragmentation on the reproductive success and genetic structure of the progeny produced by the tropical timber tree *Pachira quinata* by analyzing the following variables: (1) flower production, (2) fruit set, (3) seed production, (4) outbreeding frequency (*f*), (5) paternity correlation (*r*).
within trees (i.e., probability of full-sib progeny obtained from outcrossed sires), and (6) mean relatedness of seeds within and between fruits.

Methods

Study Area

We studied Pachira quinata in northwestern Costa Rica in the province of Guanacaste. This region is tropical dry forest according to the life-zone classification system of Holdridge (1969). The average annual rainfall is 1600 mm, and the dry season extends from December to May. Most tree species are deciduous, and their flowering peak occurs during the dry season. Tropical dry forests constitute one of the most endangered ecosystems in the world. Today, only 0.09% of the original dry forest is present in Mesoamerica (Janzen 1988), and <0.1% of Costa Rica is covered with this biome (Sánchez-Azofeifa 1996). Most of the tropical dry forest in Costa Rica has been destroyed by timber and cattle industry during the last century, and today much of this land is covered by pasture and agricultural fields (Quesada 1974; Janzen 1988; Quesada & Stoner 2003).

Selection of Trees

Pachira quinata (Bombacaceae) (Jacq.) Alversen [=Bombacopsis quinatum (Jacq. Dugand)] (Alversen 1994) is a Neotropical species distributed in the dry forest from Honduras to northern South America. It is an important timber species that has been heavily exploited because of its durable and resistant wood. P. quinata trees may grow up to 35 m in height and 2.5 m in diameter under natural conditions. Trees normally have big buttresses at the base, a gray thorny bark, and a deep central root system. Leaves are digitate compound, with glabrous, oblong leaflets (Alversen 1994). P. quinata is deciduous: leaf drop occurs in late November and new leaves are produced in early May. The flowering period extends from January to March, immediately followed by the fruiting period from April to May. Flowers are hermaphroditic and protandrous, with multi-staminate white filaments and a single central style. Anthesis takes place at dusk, and flowers last for one night. Flowers are pollinated by bats (Glossophaga soricina) and sphingid moths (Quesada et al. 2001). Each ovary contains an average of 160 ovules, and fruits produce an average of 20 seeds, which are small and wind-dispersed (Quesada et al. 2001). Fruits are dehiscent, dry, and woody. P. quinata has been classified as a self-incompatible species based on hand-pollination experiments and our previous genetic studies (Kane et al. 1993; Quesada et al. 2001). A high proportion of adult P. quinata in natural populations has been extracted for timber, but isolated trees in pastures and a few continuous populations still exist within protected areas of Guanacaste.

Sampling Design

To examine the effects of forest fragmentation on the reproductive success and genetic variation of the progeny of P. quinata, we compared isolated trees with trees in continuous populations. A tree was considered isolated if it was separated by more than 500 m from the nearest conspecific and surrounded by agricultural fields or pastures. Isolated trees were systematically selected in disturbed sites along the Panamerican Road near the Guanacaste Conservation Area. Continuous populations consisted of groups of 20 or more reproductive individuals per hectare surrounded by undisturbed mature forest. They were located within the Guanacaste Conservation Area, Costa Rica (lat. 84°37’W, long. 9°45’N, 200–250 m). Trees in continuous populations were selected from two sites located 15 km from each other within the study area.

To control for the effect of flowering phenology on the reproductive success and genetic variation of progeny of isolated and continuous populations, trees were classified according to the time of peak flowering. We determined the date of peak flowering for each individual in Julian days by counting the total number of flowers produced every 15 days during the reproductive season and then used those data to estimate an average peak flowering date for the entire population. The date of peak flowering for the entire population was estimated as the weighted mean of flowering dates of the population, where each flowering date was weighted by the number of trees blooming for each date. The date of peak flowering for each individual tree was estimated as the weighted mean of the flowering dates of each individual, where each flowering date was weighted by the number of flowers per tree for each date. Trees with peak flowering dates within 1 SD of the population mean date were classified as individuals with synchronous flowering, and the rest were classified as individuals with asynchronous flowering. Therefore, 50% of the flowers produced by trees with asynchronous flowering opened at least 3 weeks before (or after) the population’s peak flowering date.

To evaluate the reproductive success of P. quinata, we determined the total flower and fruit production and fruit set (i.e., number of fruits per flower) of each tree. Because we counted the number of flowers produced by each individual every 15 days, we estimated the total flower production of each tree as the area under the distribution obtained by the number of flowers versus time. We estimated the production of fruits of each individual tree by counting the total number of fruits produced every 15 days during the fruiting period. The total number of fruits produced by each individual was esti-
Six polymorphic enzyme systems were analyzed: leucine aminopeptidase (LAP, 3.4.11.1), shikimate dehydrogenase (SKDH, 1.1.1.25), phosphoglucoisomerase (PGI, 5.3.1.9), aspartate aminotransferase (AAT, 2.6.1.1), esterase (EST, 3.1.1.1.), and alcohol dehydrogenase (ADH, 1.1.1.1). The PGI enzyme system showed two polymorphic loci; so we used seven polymorphic loci to determine the selfing rate and genetic relatedness within *P. quinata* progenies. The genotype of adult trees was not scored because enzyme activity was resolved only in seedlings.

We estimated two genetic parameters for the population of trees in isolation and in continuous forest: multilocus outcrossing rate (*t*<sub>m</sub>) and a paternity correlation (*r*<sub>p</sub>) within trees, which was the proportion of full siblings among outcrossed siblings. The paternity correlation is also equivalent to the probability that any two randomly chosen outcrossed seeds were sired by the same father. Ritland (1989) states that the paternity correlation (*r*<sub>p</sub>) is inversely related to the number of outcross parents (*n*) by *r*<sub>p</sub> = 1/*n*, where *n* is the effective number of pollen donors (i.e., unrelated sires). These genetic parameters were estimated for the progeny of populations of maternal trees under different conditions of forest fragmentation (isolated vs. continuous populations) and flowering phenology (asynchronous vs. synchronous). We calculated genetic parameters using the models proposed by Ritland (1989) and the MLTR computer program (Ritland 1996). The standard error was calculated by bootstrapping with 1000 repetitions (Ritland 1996). To compare the genetic parameters for the populations of trees in different forest conditions, we determined the difference in outcrossing rates for each of the 1000 bootstrap trees in isolation and trees in continuous populations. We used the same procedure to compare the correlation of paternity of the progeny from trees in isolation with that of trees in continuous populations. The normality of these differences was verified, and the probability of obtaining a difference value statistically different from zero was tested with a student’s *t* test. We used the same procedure to compare the *t*<sub>m</sub> and *r*<sub>p</sub> values between trees with synchronous and asynchronous flowering phenology.

Because the estimation of the mating-system parameters of plant populations can have large variances because of variation between progenies in the number of sires, selfing rate, and biparental inbreeding, we also calculated mean levels of relatedness for individual fruits. We calculated two coefficients of mean relatedness for each fruit: (1) the mean relatedness of seed pairs within fruits and (2) the mean relatedness of seed pairs between fruits, which consisted of seeds from one fruit and seeds from other fruits within the same tree. We used a regression measure of relatedness (Queller & Goodnight 1989) as an estimate of the standard coefficient of relationship, in which an estimate of 0.25 indicates a half-sibling relationship and 0.5 indicates a full-

A sample of 20 fruits was collected from each maternal tree, and seeds from each fruit were counted and classified as either aborted or potentially viable. We collected seeds from 20 isolated trees and 20 trees in continuous populations. Aborted seeds are usually wrinkled and black, whereas potentially viable seeds are well rounded and brown. We calculated the proportion of potentially viable seed as the number of viable seeds over the total number of seeds per fruit. We used a mixed-effect analysis of variance (ANOVA) (GLM; SAS 1995) to analyze the effects of forest fragmentation and flowering phenology on the number of potentially viable seeds. Tree condition and flowering phenology were considered fixed effects, whereas maternal tree, nested within tree condition, was considered a random term. Seed number was log-transformed to achieve a normal distribution.

### Genetic Analysis

To determine the effects of forest fragmentation and flowering phenology on the genetic structure of the progeny produced by *P. quinata*, we conducted an allozyme analysis with starch-gel electrophoresis. We collected 10 fruits from each of 15 isolated trees and 15 trees from continuous populations and randomly selected four seeds from each fruit. Seeds were germinated in individual petri dishes. We extracted enzymes from homogenized hypocotyl tissue obtained 3 days after seed germination. Extraction, gel buffers, and staining protocols followed those of Weeden and Wendel (1989). Six polymorphic enzyme systems were analyzed: leucineaminopeptidase (LAP, 3.4.11.1), shikimate dehydrogenase (SKDH, 1.1.1.25), phosphoglucoisomerase (PGI, 5.3.1.9), aspartate aminotransferase (AAT, 2.6.1.1), esterase (EST, 3.1.1.1.), and alcohol dehydrogenase (ADH, 1.1.1.1). The PGI enzyme system showed two polymorphic loci; so we used seven polymorphic loci to determine the selfing rate and genetic relatedness within *P. quinata* progenies. The genotype of adult trees was not scored because enzyme activity was resolved only in seedlings.
sibling relationship. However, natural inbreeding or outbreeding and statistical error may yield estimates of relatedness for half sibs and full sibs beyond this theoretical range. In addition, natural variation of relatedness within sibling progenies can result in a continuous distribution, with values between 0 and 1. In studies with limited sample sizes, as occurs for the progeny of individual trees, regression coefficients of relatedness are statistically more robust than relatedness coefficients obtained by maximum-likelihood methods (Ritland 1989; Lynch & Ritland 1999). Regression estimates of relatedness were calculated with the computer program Relatedness 5.0 (Goodnight & Queller 1990). We used a two-way factorial ANOVA (GLM; SAS 1995) to analyze the relationship of mean relatedness between and within fruits.

Results

The duration of flowering and the mean peak flowering date were similar between tree conditions (Fig. 1). However, isolated trees (\(\bar{X} = 6655, SE = 91\)) produced more flowers per individual than trees from continuous populations (\(\bar{X} = 2357, SE = 100; F_{1,51} = 5.5, p < 0.05\); Fig. 1). Total flower production was independent of the flowering phenology of trees (\(F_{1,51} = 0.2, p = 0.65\)) and of the interaction between tree condition and flowering phenology (\(F_{1,51} = 0.04, p = 0.8498\)). Total fruit production was independent of forest fragmentation (\(F_{1,51} = 3.56, p = 0.07\)), flowering phenology conditions (\(F_{1,51} = 0.1, p = 0.75\)), and the interaction between tree condition and flowering phenology (\(F_{1,51} = 1.5, p = 0.22\)).

Fruit set was significantly greater in individuals from continuous populations than in isolated trees (\(F_{1,51} = 4.45, p = 0.039\)). On average, 6% (1.3% SE) of the flowers produced a fruit on trees from continuous populations, whereas only 3% (0.5% SE) developed into fruits on isolated trees. The flowering phenology of trees did not affect fruit set (\(F_{1,51} = 0.03, p = 0.852\)). An average of 3% (± 0.006 SE) of the flowers set fruit in trees with synchronous and asynchronous flowering. There was no significant interaction between tree condition and flowering phenology (\(F_{1,51} = 0.30, p = 0.585\)). Differences in fruit set between trees in isolation and in continuous populations were influenced mainly by the greater proportion of individuals from continuous populations, which had more than 10% of their flowers set fruit. These individuals produced intermediate to low numbers of flowers relative to the highest levels of flower production in the population (Fig. 2). Five of the 24 trees from continuous populations showed a fruit set of >10%, whereas only 1 of the 31 isolated trees had an equivalent fruit set.

An average of 24 (0.9 SE) potentially viable seeds and 9 (0.5 SE) aborted seeds were produced per fruit. The proportion of potentially viable seeds produced per fruit was independent of tree condition (\(F_{1,815} = 0.06, p = 0.807\)) and flowering phenology (\(F_{1,815} = 0.17, p = 0.681\)). The variation in the number of seeds per fruit was significantly affected by the identity of the maternal tree (\(F_{39,815} = 160.1, p < 0.001\)).

Allele frequencies from which to estimate genetic parameters were calculated from four alleles for each of two loci (LAP, SKDH), two triallelic loci (EST, AAT), and three loci with biallelic variation (PGI-1, PGI-2, ADH). The allozyme genetic analysis showed similarly high levels of expected heterozygosity for progenies of continuous populations (\(H_e = 0.398, 0.267\) SD) and isolated populations (\(H_e = 0.400, 0.210\) SD).

![Figure 1. Mean flower production in 1999 of isolated Pachira quinata and P. quinata from continuous populations, estimated as the total number of flowers produced by each individual every 15 days during the reproductive period. Bars represent standard errors.](image-url)
P. quinata was predominantly outcrossing and the proportion of outcrossed seeds showed a tendency to be greater for trees in continuous populations than for isolated trees (Table 1), but this difference was not statistically significant ($t = 1.327$, df $= 999$, $p = 0.094$). The same trend was observed for synchronous and asynchronous trees, where the proportion of outcrossed progeny showed a tendency to be greater for synchronous trees, but the difference was not statistically different ($t = 1.21$, df $= 999$, $p = 0.115$). In addition, the paternity correlation estimates suggested that isolated trees were more likely to produce full-sibling progeny within trees than were individuals from continuous populations. The difference in the paternity correlation between isolated trees and trees from continuous populations was 0.274 (0.015 SE) and was significantly different from zero ($t = -1.851$, df $= 999$, $p = 0.033$).

Two to three outcross pollen donors sired the progeny of trees from continuous populations, whereas one outcross pollen donor sired the progeny of isolated trees. Similarly, the paternity correlation of asynchronous trees was greater than that of trees with synchronous flowering ($t = 2.36$, df $= 999$, $p < 0.01$). The progeny produced by trees with synchronous flowering was sired by an average of two outcross pollen donors, whereas only a single pollen donor was represented in the progeny of asynchronous flowering trees. Mean relatedness within fruits was significantly greater for the progeny of isolated trees than for the progeny of trees in continuous populations (Fig. 3; $F_{1,147} = 6.96$, $p < 0.01$). Seed relatedness within fruits was independent of flowering phenology ($F_{1,147} = 0.33$, $p = 0.56$) and of the interaction between tree condition and flowering phenology ($F_{1,147} = 0.18$, $p = 0.66$).

Similarly, the relatedness of seeds from different fruits within trees was significantly greater for the progeny in isolated populations than for the progeny in continuous populations (Fig. 4; $F_{1,148} = 13.59$, $p < 0.01$). Seed relatedness between fruits was independent of flowering phenology ($F_{1,148} = 3.45$, $p = 0.06$) and of the interaction between tree condition and flowering phenology.

### Table 1. Outbreeding rate ($t_m$), paternity correlation ($r_p$) and number of sires, estimated as $n = 1/r_p$, for the progeny of Pachira quinata produced under different spatial and phenological conditions.*

<table>
<thead>
<tr>
<th>Trees</th>
<th>$t_m$ (SE)</th>
<th>$r_p$ (SE)</th>
<th>No. of sires</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continuous</td>
<td>0.915 (0.043)</td>
<td>0.470 (0.085)</td>
<td>2–3</td>
</tr>
<tr>
<td>Isolated</td>
<td>0.777 (0.114)</td>
<td>0.740 (0.118)</td>
<td>1–2</td>
</tr>
<tr>
<td>Synchronous</td>
<td>0.919 (0.055)</td>
<td>0.471 (0.099)</td>
<td>2–3</td>
</tr>
<tr>
<td>Asynchronous</td>
<td>0.726 (0.117)</td>
<td>0.892 (0.116)</td>
<td>1</td>
</tr>
</tbody>
</table>

*Standard errors are given in parentheses. Number of sires is the minimum and maximum number of donors.

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Figure 2. Relationship of the total flower production and fruit set for Pachira quinata in isolation and in continuous populations.

Figure 3. Mean relatedness within fruits of the progeny of Pachira quinata for trees in isolation and in continuous populations. Bars represent standard errors.
distant individuals located at low-density, disturbed sites (Ghazoul et al. 1998). Similarly, in isolated P. quinata, the low density of reproductive donors might be hindering the ability of pollinators to transfer pollen between trees, which in turn might be negatively affecting fruit set.

An additional explanation for a decrease in fruit set in isolated trees might be related to limited resources for the development of fruits. In isolated trees, the proportion of flowers setting fruit might be restricted by a threshold in the total number of fruits a tree is able to produce (Fig. 2). Evidence from other species indicates that an upper limit to fruit production is set by resources rather than flower number (Lloyd 1980; Stephenson 1981, 1992; Lee 1988).

In P. quinata, the degree of relatedness of the progeny of isolated trees was greater than that of the progeny of trees in continuous populations (Figs. 2 & 3). In contrast, the degree of relatedness was not affected by the level of flowering synchronization between trees. Levels of relatedness between fruits were positively correlated with levels of relatedness within fruits. This correlation indicates that spatial isolation affects pollen flow within individual trees and the number of pollen donors within individual flowers because uniparental paternity is more likely to occur within and between fruits of isolated trees (Table 1; Figs. 3 & 4).

Studies on the mating systems and incompatibility mechanisms of the family Bombacaceae suggest that population estimates of outcrossing rates can be influenced by different density conditions (Murawski & Hamrick 1992a, 1992b; Gribel et al. 1999). A previous study indicates that a natural population of P. quinata located in a continuous forest is self-incompatible (Quesada et al. 2001). But the results of our genetic analysis of trees from different populations located in continuous forests and in isolation suggest that partial self-compatibility in P. quinata may depend on the degree of isolation. In P. quinata and other species of the family Bombacaceae, the incompatibility reaction apparently occurs at the base of the flower style or at the ovary, but self-fertilization is not completely discarded (Baum 1995; Quesada et al. 2001). One possible explanation of our results is that P. quinata has a cryptic self-incompatibility system that allows self-fertilization when cross-compatible pollen is limited. A similar flexible-breeding system might be operating in other Bombacaceous trees (Murawski & Hamrick 1992a, 1992b; Gribel et al. 1999). Ceiba pentandra and Cavanillesia platanifolia have low outcrossing rates similar to those of the isolated and asynchronous trees of P. quinata (Murawski & Hamrick 1992a, 1992b). Murawski and Hamrick (1992b) suggest that C. platanifolia and C. pentandra have high levels of selfing (possibly geitonogamy) because of the high density of flowering per individual, the amount of pollen available from other trees, and the number of pollen donors available. More generally, our results are supported by

Figure 4. Mean relatedness between fruits of Pachira quinata of the progeny of isolated trees and trees in continuous populations. Bars represent standard errors.

\[(F_{1,148} = 1.69, p = 0.19)\]

Estimates of mean relatedness between and within fruits were significantly correlated \((r_p = 0.245, t_{146} = 3.03, p < 0.0020)\).

Discussion

Our results indicate that in P. quinata, isolated trees produced twice the flowers of trees in continuous populations. Although trees from both density conditions were similar in stem diameter, isolated trees tended to develop crowns with more reproductive branches than individuals in the forest because they were found in open areas where there was no competition from neighbors. However, total fruit production was similar between tree conditions. This apparent contradiction is explained by the fact that fruit set was negatively affected by forest fragmentation. Two trees in continuous populations produced fewer flowers (900–1200) but were able to develop a high proportion (15–25%) of them into mature fruits. Trees with similarly high levels of fruit set were found in another naturally continuous population of P. quinata in Costa Rica (Quesada et al. 2001). A possible explanation for these results is that pollination with compatible pollen is hindered in fragmented habitats, thereby limiting the ability of individuals to achieve high levels of fruit set. In agreement with our results, other researchers have found a positive relationship between fruit set and forest-fragment size, (Aizen & Feinsinger 1994a; Ghazoul et al. 1998; Cunningham 2000b). For example, Shorea siamensis, another tropical dry-forest tree, shows a reduction in fruit set as a result of limited transfer of compatible pollen between
findings that a flexible breeding system of dipterocarps is affected by forest fragmentation and logging (Murawski et al. 1994; Ghazoul et al. 1998; Ile 2000).

Pollinator behavior might also help explain the mating patterns of *P. quinata*. In fragmented habitats or in trees with an early or late flowering peak, bat pollinators are more likely to promote selfing within trees (i.e., geitonogamy) because they will tend to forage within the same tree where nectar is concentrated. One of the main pollinators of *P. quinata*, the long-tongued bat (*Glossophaga soricina*), adopts a territorial behavior within a single plant in disturbed, isolated environments with limited resources (Lemke 1984, 1985). This same behavior is likely to restrict the number of donors carried in the pollen loads that bats move between flowering trees. Our results indicate that trees in spatial isolation have a tendency to produce singly sired fruits, whereas in undisturbed natural forests multiple paternity is more common.

Our results suggest that forest fragmentation reduces the number of pollen donors represented in the progeny of *P. quinata*, an important tropical tree species of rare and diminishing dry-forest habitat. Total fruit production was not affected by forest fragmentation or flowering phenology. Although isolated trees produced more flowers, the total production of fruits per individual was equivalent between the two tree conditions because fruit set was higher in continuous populations. The progeny produced by trees in continuous populations were less related to each other than progeny from isolated trees because there were more sires and higher levels of outcrossing in continuous populations. Even though *P. quinata* is a relatively common tree in the dry tropical forest in Costa Rica, forest fragmentation has an effect on the distribution of the genetic variability within populations. Fragmentation is reducing genetic variability within the progenies of isolated trees, and thus increasing the variation between progenies of different trees in the same populations. Trees in isolation appear to be producing a comparable quantity of viable seeds compared with trees in continuous undisturbed habitats, but the progeny of isolated trees represent a limited sample of the genetic diversity of the original natural populations, which will have unknown consequences on the fitness and the regeneration ability of seeds produced by these remnant populations. In using the genetic resources of the tropical forest and in implementing forestry-management plans, managers need to consider an assessment of complex spatial and temporal factors that affect the reproduction and breeding system of tropical tree populations.

**Acknowledgments**

We thank K. Stoner and T. Robles for making valuable comments that significantly improved previous versions of this paper. We are grateful to T. Robles, A. Quesada, J. Breitling, P. Aguilar, and K. Stoner for their valuable help and assistance in the field and in the laboratory. We also thank M. M. Chavarria, F. Chavarria, R. Blanco, and S. Marin from the Área de Conservación Guanacaste for logistical support. This study was performed in partial fulfillment of the requirements of the M.S. degree of E.J.F. at the University of Costa Rica. This research was partially funded by Consejo Nacional de Ciencia y Tecnología, Mexico (CONACyT) (research grant 31826N); Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT), Universidad Nacional Autónoma de México (research grant IN213999); Universidad de Costa Rica (research grant 111–99–319); Programa de Cooperación México–Costa Rica (research grant 302CR075 awarded to M. Quesada, K. Stoner, and J. Lobo); International Foundation for Science (grant D/2617–2 awarded to M.Q.; and the Idea Wild Organization (grant awarded to E.J.F.).

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