Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America

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ABSTRACT. Breeding systems and dispersal mechanisms of plants ($\geq$ 2.5 cm dbh) were examined in fragments of tropical dry forest in Central America to identify life-history characteristics associated with rarity. In particular, the richness and abundance of dioecious and mammal-dispersed trees and shrubs were examined to identify potential associations with precipitation, anthropogenic disturbance, and area. Plots totalling 1000 m^2 per site were established in seven nature reserves in Costa Rica (two sites) and Nicaragua (five sites). Overall, tropical dry forests of Central America have a similar proportion of dioecious species to other lowland neotropical forests and a similar proportion of wind-dispersed plants to other tropical dry forests around the world. However, the number of dioecious and mammal-dispersed species declined with decreasing forest cover within each reserve. Although dioecious species were rare in smaller forest fragments, some of these species will not be threatened with regional extinction because they are early successional plants, they have large geographic ranges, and they are not restricted to the tropical dry forest life zone. Mammal-dispersed plants were rare in small fragments, but it is not clear whether this was due to the loss of dispersal vectors or other life-history characteristics.

KEY WORDS: Breeding systems, Central America, dioecy, seed dispersal, rarity, tropical dry forests, zoochory

INTRODUCTION

Tropical dry forest in Central America once extended along the Pacific coast from sea level to 400 m from Guatemala to Costa Rica with a disjunct patch in Panama (Murphy & Lugo 1995, Sabogal 1992). However, rich soils, the ability to burn though a prolonged dry season, and agricultural expansion have resulted in a large reduction in their original cover (Murphy & Lugo 1986). Today, tropical dry forests have been reduced to less than 0.1% of their original extent on the Pacific side of Central America and are considered by some to

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be the most endangered ecosystems in the lowland tropics (Janzen 1988a, Lerdau *et al.* 1991).

There are surprisingly few published studies on the effects of forest fragmentation on the diversity of woody plants in the tropics, but there is no shortage of theories for why certain plant species become extinct in habitat fragments (Ackerly *et al.* 1990, Howe & Smallwood 1982, Janzen 1986, Jordano 1995, Nason *et al.* 1998, Turner 1996). Janzen (1986) referred to severely fragmented tropical forests as the 'living dead' because many of the trees, which have long generation times, may eventually become extinct as co-adapted pollinators and seed dispersers become locally extinct.

An empirical study by Meave & Kellman (1994) found that natural fragments of riparian forest in Belize appeared depauperate in dioecious and mammal-dispersed plants compared with continuous forest. The authors reported a 16.5% incidence of dioecy for trees in natural riparian forest fragments compared with 23 to 40% dioecy recorded from continuous forest in the lowland neotropics (Bawa *et al.* 1985, Bawa & Opler 1975). This suggests that fragmentation may have a deleterious effect on dioecious plants and that dioecy may be disadvantageous in isolated habitats (Meave & Kellman 1994). Plant species exhibiting certain dispersal modes may also be more vulnerable to local extinction with increasing fragmentation. The extinction of large mammals and birds in successively smaller fragments of tropical forest has been well documented (Bierregaard *et al.* 1992, Diamond *et al.* 1987, Turner 1996), while the secondary extinction of vertebrate-dispersed plants, although often proposed, is poorly documented (Harrington *et al.* 1997, Howe 1984, Howe & Smallwood 1982). Janzen (1988b) noted that regeneration of tropical dry forests in Santa Rosa, Costa Rica were dominated by wind-dispersed trees that would persist for hundreds of years and remain unattractive to vertebrate dispersers. Because there are nearly three times as many vertebrate-dispersed species as wind-dispersed ones in Santa Rosa, vertebrate-dispersed plants may be the most extinction-prone group in small habitat fragments (Janzen 1988b, Janzen & Liesner 1980).

This analysis of tropical dry forest has two primary objectives: (1) to summarize richness and abundance of the breeding systems and dispersal mechanisms of woody plants in Central American tropical dry forest, (2) to identify environmental variables, such as area, precipitation, or anthropogenic disturbance, associated with rarity in breeding systems and dispersal mechanisms of trees and shrubs.

STUDY AREA

Study sites were located in seven fragments of tropical dry forest in Costa Rica and Nicaragua. All sites are decreed conservation areas. Study sites include: (1) Santa Rosa National Park, Costa Rica (10°50′N, 85°40′W), (2) Palo Verde National Park, Costa Rica (10°20′N, 85°20′W), (3) La Flor Nature Reserve,

Nicaragua (11°8′N, 85°47′W), (4) Chacocente Wildlife Refuge, Nicaragua (11°32′N, 86°12′W), (5) Reserve on the island of Ometepe, Nicaragua (11°32′N, 85°37′W), (6) Masaya National Park, Nicaragua (11°58′N, 86°06′W), and (7) Cosiguina Nature Reserve, Nicaragua (12°54′N, 87°32′W). These fragments were all defined as tropical dry forest according to the Holdridge life zone system and are the best remaining patches of tropical dry forest in Central America (Holdridge *et al.* 1971).

METHODS

Plots totalling 1000 m^2 were established at each site following Gentry (1982, 1988) without modifications. Each sample consists of 10 transects (2-m × 50-m) in which all plants of 2.5 cm dbh or greater (>2.5 cm diameter for lianas) which are rooted in the sample area were censused (Gentry 1982, 1988). Each site was visited a minimum of three times from June 1996 to July 1997 to ensure the collection of fertile voucher specimens. All voucher specimens were deposited in the herbaria of the Universidad Centroamericana (UCA) in Managua and the University of California, Los Angeles (LA).

All plants were classified into three breeding categories: hermaphroditic, monoecious, and dioecious following Bawa *et al.* (1985) and Bullock (1985). The hermaphrodite category (bisexual flowers) includes all monostylous and heterostylous hermaphroditic species. The monoecious category (male and female flowers on the same plant) includes all andromonoecious, polygamo-monoecious, and strictly monoecious species. The dioecious category (male and female flowers on different plants) includes all androdioecious and strictly dioecious species.

Dispersal types were classified into four categories and one sub-category: anemochory, zoochory (sub-category: mammal-dispersed), autochory, and diplochory (van der Pijl 1982). Anemochorous species are wind-dispersed plants that generally have winged or plumose seeds. Zoochorous species are vertebrate-dispersed plants with a fleshy exocarp. The mammal-dispersed sub-category includes all plants with fleshy fruits (>2 cm) or plants classified as dispersed by large mammals in Gentry (1982) and Janzen & Martin (1982). Autochorous species are plants that have explosive pods or capsules that usually disperse the seed. Diplochorous species are plants that have the ability to be dispersed by two different modes, i.e. autochory and zoochory.

Spearman's rank correlations were used to search for associations between breeding system and dispersal mechanism of trees/shrubs and environmental variables. Environmental data on area, annual precipitation, and anthropogenic disturbance were collected for all sites (Table 1). Two types of aerial data were collected: (1) the area of the decreed Nature Reserve, and (2) the area of forest cover within each reserve. Data on reserve size are relatively straightforward and available from a number of sources (Hartshorn 1983,

Table 1. Environmental variables for seven tropical dry forest sites in Central America.

Sites	Reserve size (ha)	Forest cover (ha)	Precipitation (mm)	Anthropogenic disturbance
Palo Verde	17 993	1646	1717	4
Cosiguina	12 420	5132	1827	9
Santa Rosa	10 800	3556	1552	3
Masaya	5100	1300	1251	8
Chacocente	4800	1500	1362	5
La Flor	800	449	1805	5
Ometepe	420	420	1695	6

IRENA 1990, Maldonado *et al.* 1995). The area of tropical dry forest and semi-deciduous forest within each reserve came from a variety of sources (Gillespie & Martínez 1996, Kramer 1997, Maldonado *et al.* 1995, MARENA 1997, Sabogal 1992). Data on annual precipitation over 15 y were collected from weather stations in or near each site except for La Flor and Ometepe, which have only 6 y of data (INETER 1997, Janzen *pers. comm.*, Maldonado *et al.* 1995).

Fire, wood collection, and grazing by livestock are the most important anthropogenic disturbances in tropical dry forest (Murphy & Lugo 1986). All sites are ranked by levels of anthropogenic disturbance following Veblen *et al.* 1992 (degree of browsing in three classes, severity of wood collection in three classes, and frequency of fire in three classes). Sites with low levels of anthropogenic disturbance have low rankings while sites with high levels of disturbance have high rankings (Table 1).

RESULTS

A total of 1484 individuals comprising 204 species and morphospecies were encountered from seven sites with an average of 212 individuals (range 134 to 264 individuals) or 56 species per site (range 44 to 75 species). The number of species at each site tended to level off after the eighth or ninth transect, as noted in other tropical dry forests in which the same method was used (Keel *et al.* 1993). Approximately 73% of these plants were classified as trees and shrubs (149 spp.) and 27% were lianas (55 spp.).

Breeding systems

Hermaphroditic plants represented the most common breeding system in tropical dry forests accounting for 64.2% of all species encountered from all sites (Table 2). There were 15.7% dioecious species and 14.2% monoecious ones from all sites. The breeding systems of 12 species could not be positively determined and were classified as unknown. Trees and shrubs had a higher incidence of dioecy (20.1%) than lianas (3.6%). Santa Rosa and Palo Verde had the highest numbers of dioecious trees and shrubs while La Flor, Ometepe, and Chacocente had the lowest (Table 3). The proportion of dioecious plants

Table 2. *Number of species of lianas, and trees and shrubs encountered in seven tropical dry forests in Central America.*

Breeding systems	Total species	Lianas	Trees and shrubs
Hermaphroditic	131	41	90
Monoecious	29	8	21
Dioecious	32	2	30
Unknown	12	4	8
Total	204	55	149

Table 3. *Breeding system of tree and shrubs based on species richness and abundance from seven tropical dry forest sites.*

	Sites[1]						
Breeding systems	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Number of species							
Hermaphroditic	22	32	25	30	22	31	15
Monoecious	5	6	7	6	3	4	5
Dioecious	11	15	13	6	8	6	6
Unknown	0	1	2	1	0	4	0
Total	38	54	47	43	33	45	26
Number of individuals							
Hermaphroditic	82	105	72	122	113	173	49
Monoecious	10	18	61	36	16	9	24
Dioecious	26	44	48	16	94	14	33
Unknown	0	2	2	3	0	6	0
Total	118	169	183	177	223	202	106

[1] Cos. = Cosiguina, S.R. = Santa Rosa, P.V. = Palo Verde, Chac. = Chacocente, Mas. = Masaya, L.F. = La Flor, Ome. = Ometepe.

at all sites ranged from 13 to 29%. The hermaphroditic breeding system was the most abundant by number of individuals of trees and shrubs at all sites, with dioecy the second most abundant breeding system at five sites. The hermaphroditic lianas were the most abundant by number of species and number of individuals at all sites followed by monoecy. There were only two species of dioecious liana (*Pisonia aculeata* and *Tetracera volubilis*) encountered in Santa Rosa and Cosiguina.

Dispersal mechanisms

Zoochory was the most common dispersal type in Central American tropical dry forests, accounting for *c.* 45% of all species encountered (Table 4). Anemochory was the second most common mechanism, accounting for 38% of all species. Autochory and diplochory were relatively rare. Within the zoochory category, mammal-dispersed plants accounted for 16.7% of all species. For trees and shrubs, zoochory was the most common form of dispersal (55%), followed by anemochory (27.5%). Amongst the sites, Santa Rosa had the most zoochorous and mammal-dispersed trees and shrubs (Table 5). Zoochorous trees and shrubs were the most abundant in terms of both number of species and individuals at all sites except La Flor, which had a high number of wind-dispersed species and individuals. Anemochorous lianas were dominant based

Table 4. *Number of species of lianas, and trees and shrubs encountered in seven tropical dry forests in Central America.*

Dispersal mechanisms	Total species	Lianas	Trees and shrubs
Autochory	6	1	5
Anemochory	78	37	41
Zoochory	92	10	82
(Mammal-dispersed)	(34)	(0)	(34)
Combination	15	2	13
Unknown	13	5	8

Table 5. *Dispersal mechanism of tree and shrubs based on species richness and abundance from seven tropical dry forest sites. Abbreviations of sites are the same as in Table 3.*

	Sites[1]						
Dispersal mechanisms	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Number of species							
Autochory	0	2	2	1	1	0	1
Zoochory	23	34	24	24	19	17	17
(Mammal)	(12)	(17)	(10)	(9)	(6)	(10)	(3)
Anemochory	7	13	15	11	9	20	6
Combination	7	4	4	6	4	5	2
Unknown	1	1	2	1	0	3	0
Total	38	54	47	43	33	45	26
Number of individuals							
Autochory	0	14	4	1	1	0	3
Zoochory	55	77	107	91	121	33	76
(Mammal)	(31)	(36)	(44)	(32)	(27)	(23)	(13)
Anemochory	34	62	52	60	51	127	24
Combination	27	14	18	22	50	37	3
Unknown	2	2	2	3	0	5	0
Total	118	169	183	177	223	202	106

on number of species and individuals at all sites. There were no mammal-dispersed lianas.

Environmental correlates

Spearman's rank correlations identified environmental variables associated with breeding systems and dispersal mechanisms of trees and shrubs (Table 6). For breeding systems, the number and percentages of dioecious species encountered at each site were significantly correlated with both reserve size and forest cover. There was no correlation between species richness of dioecious plants, percentage occurrence, or number of individuals, with precipitation or disturbance. However, the number of hermaphrodite species was negatively correlated with disturbance. For dispersal mechanisms, the number of zoochorous species was not significantly correlated with forest cover, reserve size, precipitation, or disturbance. The number and percentage of mammal-dispersed plants was positively correlated with forest cover, while the abundance of mammal-dispersed plants was positively correlated with reserve size. There was no correlation between the species richness of anemochorous plants,

Table 6. Spearman's rank correlations for plant breeding systems and dispersal mechanisms of trees and shrubs, and environmental variables: reserve area (RS), forest cover (FC), precipitation (PR), and anthropogenic disturbance (AD).

Variables	RS	FC	PR	AD
Breeding systems	0.144	0.288	−0.036	−0.764*
Number of hermaphrodite species				
Proportion of hermaphrodite species	−0.429	−0.179	−0.393	0.018
Number of hermaphrodite individuals	−0.250	−0.107	−0.214	−0.090
Number of dioecious species	0.852*	0.778*	0.074	−0.374
Proportion of dioecious species	0.829*	0.811*	0.252	0.109
Number of dioecious individuals	0.464	0.143	−0.464	−0.054
Dispersal mechanisms				
Number of anemochorous species	0.214	0.071	0.143	−0.703
Proportion of anemochorous species	−0.036	−0.357	−0.107	−0.414
Number of anemochorous individuals	0.000	0.071	−0.036	−0.685
Number of zoochorous species	0.673	0.739	−0.236	−0.587
Proportion of zoochorous species	−0.143	0.071	−0.179	0.216
Number of zoochorous individuals	0.357	0.071	−0.750	−0.144
Number of mammal-dispersed species	0.631	0.811*	0.451	−0.391
Proportion of mammal-dispersed species	0.505	0.775*	0.559	−0.118
Number of mammal-dispersed individuals	0.821*	0.750	−0.071	−0.595

*$P < 0.05$.

percentage occurrence, and number of individuals, with area, precipitation or disturbance.

DISCUSSION

Plant sexuality

Central American tropical dry forest does not appear to have a significantly lower proportion of dioecious plants compared with other neotropical sites. Results from this study found 20.1% dioecy for all trees and shrubs encountered from seven sites in Central America. This is comparable to the proportion of dioecious trees (23.9%) found in the tropical dry forest of Chamela, Mexico (Bullock 1985). Approximately 21.3% of medium to large sized trees from the moist forest of Barro Colorado Island, Panama were dioecious (Bullock 1995, Croat 1978). Approximately 23.1% of lowland rainforest trees at La Selva, Costa Rica were dioecious (Bawa *et al.* 1985). As species diversity increases from dry to wet forest, it appears that tree breeding systems in lowland neotropical forests all have a relatively similar proportion of dioecious species.

Bullock (1985), using the same plot method employed in this study, found that the frequency of breeding systems was remarkably similar for three 1000 m^2 plots in Chamela, Mexico. However, I found that species richness and the proportion of dioecious species varied between fragments of tropical dry forest in Central America. The number and the proportion of dioecious species at each site decreased with both reserve size and forest cover. In theory, a dioecious breeding system promotes cross-pollination and ensures genetic heterozygosity within a population (Endress 1994). If there is a low density of

dioecious individuals in a forest fragment there is a high probability that pollination will not occur (Mack 1997). Furthermore, sex-ratios of male and female individuals may also significantly hinder pollination in forest fragments (Ackerly *et al.* 1990). At this scale, these results suggest that the dioecious breeding system is rare in successively smaller patches of tropical dry forest. All the fragments in this study have been isolated for over 100 y which should have been adequate time for a number of dioecious tree and shrub species to become locally extinct or rare. Furthermore, the fragments in this study are spread over a large geographic area and are some of the only remaining protected fragments of tropical dry forest in Central America.

Caution should be taken when interpreting the conservation value of using dioecy as an indicator of plants prone to extinction. First, there are a number of physiological (self-incompatibility), structural (heterostyly), and developmental (dichogamy) phenomena in hermaphrodite flowers, that functionally result in a breeding system similar to dioecy (Endress 1994). For instance, some self-incompatible species require pollen from another individual to reproduce and these species may also be prone to local extinction in small habitat fragments. Unfortunately, there is currently not enough information on levels of self-incompatibility or other structural and developmental phenomena in tropical dry forest plants to determine whether they are as vulnerable as dioecious species. Second, when examining the list of dioecious species in tropical dry forests (Table 7), a number of species may never be vulnerable to regional extinction in Central America because of other natural history characteristics not associated with rarity, such as successional status, geographic range, and habitat preference (Rabinowitz *et al.* 1986). Dioecious species, such as *Diospyros nicaraguensis*, *Cecropia peltata*, *Bernardia nicaraguensis*, *Myriocarpa bifurca* and *Urera baccifera* are primary and early successional plants and although they may be rare in late-successional tropical dry forests, they are common in disturbed forests and landscapes. Almost all dioecious trees and shrubs in this study have an extremely wide geographic distribution into Mexico and South America. Only four dioecious species (*Bernardia nicaraguensis*, *Neea fagifolia*, *Ateleia herbert-smithii* and *Agonandra macrocarpa*) encountered in this study are restricted to Central America. Finally, most of these species are not restricted to the tropical dry forest life zone and can be found in moist forest or in light gaps in wet forest (Croat 1978, Hartshorn 1983).

Plant dispersal

The percentage of zoochorous and anemochorous plants from this study are similar to other data from tropical dry forests. In 12 neotropical dry forest sites, Gentry (1995) found that nearly 80% of all lianas and a third of all trees and shrubs were wind-dispersed. Other tropical dry forest in Asia, Australia, and Africa generally contain between 27 to 38% wind-dispersed species of trees and shrubs (Kahn & Lawrie 1987, Parthasarathy & Karthikeyan 1997, Sussman & Rakotozafy 1994). However, when compared to the tropical moist and

Table 7. Incidence of dioecious trees and shrubs in seven tropical dry forest sites. Abbreviations of sites are the same as in Table 3.

Scientific name	Total	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Bursera simaruba	7	x	x	x	x	x	x	x
Simarouba amara	6		x	x	x	x	x	x
Cordia panamensis	4	x	x	x				x
Diospyros nicaraguensis	4	x			x	x	x	
Astronium graveolens	3		x	x			x	
Spondias purpurea	3	x	x	x				
Cecropia peltata	3	x				x		x
Bernardia nicaraguensis	3		x	x		x		
Margaritaria nobilis	3			x		x		x
Chlorophora tinctoria	3	x	x	x				
Trichilia americana	2		x	x				
Pisonia macranthocarpa	2	x	x					
Neea fagifolia	2	x						x
Triplaris melaenodendron	2			x			x	
Genipa americana	2		x				x	
Randia monantha	2		x	x				
Spondias radlkoferi	1			x				
Cordia collococca	1			x				
Bursera graveolens	1					x		
Ateleia herbert-smithii	1		x					
Castilla elastica	1	x						
Brosimum alicastrum	1	x						
Agonandra macrocarpa	1				x			
Coccoloba floribunda	1			x				
Alibertia edulis	1		x					
Zanthoxylum monophyllum	1			x				
Zanthoxylum setulosum	1		x					
Alvaradoa amorphoides	1					x		
Myriocarpa bifurca	1	x						
Urera baccifera	1	x						

wet forests, the proportion of wind-dispersed species dramatically declines with increased precipitation (Gentry 1988).

No correlation exists between area of fragment and the number of zoochorous species and individuals. It would appear that frugivores (birds, bats and rodents) are able to disperse seeds whose fruits have a fleshy exocarp adequately in both small and large forest fragments. A correlation exists between forest cover and the number of mammal-dispersed species, thus it would appear the mammal-dispersed plants are more vulnerable to local extinction than are plants with other modes of dispersal. Complete floras of tropical dry forest reserves in Central America could be used to verify these results, but few such floras exist. Santa Rosa had 17 mammal-dispersed species in a 0.1-ha plot and the flora of Santa Rosa includes all but one of the mammal-dispersed species recorded from all seven sites (Janzen & Liesner 1980). Ometepe, the smallest fragment, contains only three of the 34 mammal-dispersed species. The flora of tropical dry forest at Ometepe contains only ten of the mammal-dispersed species recorded from all seven sites (Gillespie & Martínez-Sánchez 1996). This suggests that mammal dispersed species may be rare in smaller fragments.

Table 8. Incidence of mammal-dispersed trees and shrubs in seven tropical dry forest sites. Abbreviations of sites are the same as in Table 3.

Scientific name	Total	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Spondias mombin	6	x	x	x		x	x	x
Guazuma ulmifolia	5	x	x	x	x		x	
Diospyros nicaraguensis	4	x				x	x	x
Annona purpurea	4	x	x	x	x			
Astronium graveolens	3		x	x			x	
Annona reticulata	3	x				x		x
Spondias purpurea	3	x	x	x				
Chlorophora tinctoria	3	x	x	x				
Randia monantha	2		x	x				
Guettarda macrosperma	2		x					
Jacquinia nervosa	2		x		x			
Zizyphus guatemalensis	2			x	x			
Genipa americana	2		x				x	
Licania arborea	2		x			x		
Enterolobium cyclocarpum	2	x	x					
Ficus ovalis	2	x						x
Manilkara zapota	2		x				x	
Sideroxylon capiri	2				x	x		
Capparis pachaca	1				x			
Apeiba tibourbou	1	x						
Caesalpinia coriaria	1				x			
Bunchosia cornifolia	1			x				
Bactris guineensis	1				x			
Byrsonima crassifolia	1					x		
Acacia farnesiana	1	x						
Alibertia edulis	1		x					
Spondias radlkoferi	1			x				
Sapranthus palanga	1						x	
Pithecellobium saman	1	x						
Brosimum alicastrum	1		x					
Ficus sp. (G1451)	1						x	
Ximenia americana	1				x			
Agonandra macrocarpa	1		x					
Randia sp. (G1372)	1						x	

Although the results from this study found a correlation between the area of forest cover within each fragment and number of mammal-dispersed trees and shrubs, one cannot automatically assume that it is due to a loss of seed vectors. First, the list of mammal dispersed trees and shrubs (Table 8) was created following Janzen & Martin (1982) and Gentry (1982). It is the most accurate list of plants dispersed by large mammals that can be compiled based on current evidence, yet there are currently no empirical data on obligate dispersal by mammals in tropical dry forests of Central America. Most data on seed dispersal in tropical forests are casual anecdotes of birds and mammals often based on one or two tree species or individuals (Howe & Smallwood 1982). Most fruits are eaten and dispersed by many species of animals, not one or a few. Second, there is little evidence that the low numbers of mammal-dispersed plants in small fragments are due to the extinction of native tropical dry forest mammals. Domestic horses and cattle disperse many of the same plants as large native mammals (Janzen & Martin 1982). Historically, cattle

may have been the dominant large mammal in the tropical dry forest region of Central America over the last one hundred years (Parsons 1983). This may have had a more profound effect on contemporary forest composition than the recent extinction of native fauna (Janzen & Martin 1982). Finally, it may be that a majority of the mammal-dispersed trees and shrubs are rare because of a correlation between seed size and successional status of forest trees (Hammond & Brown 1995). The large-seeded plants may be rare because most are generally late successional and occur only in mature forest (Whitmore 1990). These large-seeded plants may occur in low densities in smaller or more disturbed fragments.

In conclusion, these results support Meave & Kellman's findings (1994) that dioecious and mammal-dispersed plants are rare in smaller fragments of tropical forest. Research in other fragmented tropical dry forest regions is needed to determine whether these findings are simply a local phenomenon or a general biogeographic pattern. Rather than establishing plots, recording the total number of dioecious and large-seeded trees and shrub individuals within a fragment may be the best method to test this hypothesis.

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