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Plant Reproductive Ecology of a Secondary Deciduous Tropical Forest in Venezuela

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ABSTRACT

The breeding systems, reproductive efficacies, and densities of selected trees, shrubs, vines, and hemiparasites of a secondary deciduous mid-elevation tropical forest in Venezuela are investigated. A total of 77.17 percent of the species studied are adapted for obligate outbreeding, 54.45 percent through the possession of genetic self-incompatibility, and 22.72 percent by way of dioecy or functional dioecy. Reproductive densities (density of flowering individuals) vary from 2.0 to 165.9 individuals per species per hectare with a mean of 10.7 and median of 5.0. Hemiparasites and vines form denser populations than do trees and shrubs. The densities of tree and shrub species are similar. All species, whether obligately outbred or genetically self-compatible, set abundant seed under the ecological conditions of the community. Distance between the individuals of a population does not limit seed set under obligate outbreeding. The reproductive efficacies of dioecious species are higher than those of genetically incompatible hermaphrodites. Non-autogamous compatible hermaphrodites set a lower percentage of seed than do autogamous hermaphrodites.

The proportion of outbreeding species in the secondary tropical forest is similar to that reported for a speciose tropical deciduous forest in Costa Rica; however, the species of the secondary forest exhibit higher reproductive efficacies. Factors favoring the maintenance of high proportions of obligately outbred species in species-rich tropical ecosystems are discussed.

RECENT INFORMATION and interest on coadaptations between plants and animals for pollination have produced a wealth of speculation and many perhaps-premature conclusions concerning the breeding systems of tropical plants. Fedorov (1966) proposed a novel explanation for high species diversity in tropical ecosystems based on accelerated speciation resulting from genetic drift in small isolates of predominantly self-fertilized plants. Baker (1959), stressing the hindering effect low population density and structural complexity might have on inter-individual pollinator movement, and hence cross-pollination, argued for self-compatibility in tropical plants. Percival (1974) recently inferred autogamy in 33 species in tropical scrub in Jamaica, this inference was, however, in the absence of appropriate genetic tests. It is not surprising that controlled experimental work on the breeding systems of tropical plants on an ecosystems basis is essentially lacking, for such studies have rarely been attempted in low-diversity temperate communities. In the one landmark tropical study that exists to date, Bawa (1974) demonstrated high percentages of self-incompatibility and dioecism among the trees of a lowland deciduous forest in Costa Rica.

This paper reports breeding system studies and other aspects of plant reproductive ecology of a secondary deciduous forest in Venezuela. We initiated the study with several objectives in mind: firstly, to obtain breeding system data on a community basis; secondly, to test whether intra-specific population density affects inter-individual pollinator movement and hence seed set under obligate outbreeding, and thirdly, to determine the kinds of pollinator strategies which occur in the secondary tropical forest.

CLIMATE AND ECOLOGICAL HISTORY OF STUDY SITE

All experimental work was conducted in the Biological Reserve (Arboretum de la Escuela de Biología Universidad Central de Venezuela), Colinas de Bello Monte, Edo. Miranda, Venezuela (elevation ca. 1100 m, 10° 30' N, 66° 53' W), which is part of the low mountainous area fringing the southwestern side of the Valley of Caracas. The reserve contains two hectares of continuous, secondary deciduous forest (Tropical Dry Premontane Forests, Holdridge *et al.* 1971), considered successional (Ewel and Madriz 1968), consisting of two poorly defined strata: 1) a tree strata of 5-8 m height with no single dominant, and 2) a lower strata of shrubs, herbaceous perennials, and intermixed agavaceous and cactaceous succulents, these last probably representing elements of

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the original colonizing vegetation. A total of 93 phanerogams have been collected on the site to date. This number includes 22 tree species, legumes predominating. Twenty four percent and 26 percent of the total species count are constituted by herbaceous vines and perennials, respectively. Many of the herbaceous perennials are weedy invaders, having colonized recently cut trails.

The climate of the Valley of Caracas is distinctly seasonal with 762 mm average annual precipitation (data from UCV Weather Station, Caracas). The dry season extends from December through April, with maximum monthly precipitation (110 mm) occurring in August. With a few exceptions the trees and shrubs are deciduous, leaf-fall corresponding with the onset of the dry season. Details of phenology will be presented elsewhere.

The vegetation of the Valley of Caracas has undoubtedly been dramatically altered in historical times; however, the composition of the original vegetation is not known, as accurate records do not exist. Pittier (1936) mentions virgin forest in the area during the late 1800s. The forest is compared to species-rich evergreen premontane vegetation (Tropical Premontane Wet Forest, Ewel and Madriz 1968) still extant some 85 km NW on the Cordillera de la Costa's seaward flanks, Edo. Aragua. While remnants of this vegetation type containing *Anacardium excelsum*, *Erythrina fusca*, and *Triplaris caracasana* occur in wetter sites with deep soils, we seriously doubt its existence on the xerophytic lateritic soils of the study site. Recent vegetation records are more reliable. Tamayo (1943) describes cutting, clearing, and extensive soil erosion in the study site area as late as 1936-37. The present young secondary vegetation, containing few trees exceeding 20 cm DBH, is thus probably less than 40 years old.

METHODS

BREEDING SYSTEMS.—Species were selected to include all life-forms represented, except weedy, edge perennial, annual, and occasional epiphytic species. The final choice of species was based on relative importance, adequate flowering, and a sufficiency of individuals for the tests performed. We consciously included both wet- and dry-season flowering species. The 22 species studied in detail (table 1) include 63 percent of the tree species on the site.

Four tests were performed. Individuals were tested for (1) GENETIC SELF-INCOMPATIBILITY by hand self-pollinating freshly opened flowers, previously isolated in the bud stage, and later monitoring the treated branches for fruit and seed set. Inflorescences

or individual flowers were isolated 2-15 days prior to pollination in bags made from Vyleen. Pollen for selfing was taken from the same flower or from other isolated flowers on the same plant and applied to stigmas previously checked for receptivity with a hand-lens. The pollinated flowers were tagged and rebagged until corolla drop or signs of fruit formation appeared. The percentage of flowers forming fruits and the number of seeds per fruit were recorded in this and in all subsequent tests described. Additionally, seeds were carefully checked for embryo formation. All species were checked for (2) AUTOMATIC SELF-POLLINATION. Large numbers of flowers were isolated in pollination bags between bud stage and corolla drop and later checked for fruit and seed formation. In order to distinguish between seeds produced by way of fertilization and (3) APOMIXIS, additional unopened flowers were bagged, emasculated upon anthesis, rebagged and observed for fruit and seed formation. Estimates of grades of self-incompatibility were facilitated by comparing fruit and seed set following controlled self- and cross-pollination. The procedure for (4) CROSS-POLLINATION involved prior bagging of flowers of the ovulate parent, emasculation prior to anther dehiscence, checking for stigma receptivity, and the transferal of pollen from a number of different individuals of the same species to the stigmas. The tagged flowers were rebagged and later monitored for fruit and seed set.

Two indices are employed to describe the breeding systems: 1) An INDEX OF SELF-INCOMPATIBILITY (ISI, table 2) was calculated by dividing the average number of seed set per flower hand-selfed by the same following hand cross-pollination. Self-compatible species accordingly score 1, incompletely compatible species take the values between 1 and 0, while self-incompatible species score 0.2. An INDEX OF AUTOMATIC SELF-POLLINATION (IAS, Table 3) was obtained for self-compatible species by comparing percent fruit set following automatic selfing and controlled selfing. Fully autogamous plants score 1, while partially autogamous plants take the values between 1 and 0. Self-compatible species mechanically prevented from intra-flower selfing score 0. In addition, seed set per fruit following controlled self-pollination and controlled cross-pollination is compared for self-compatible species (table 4).

REPRODUCTIVE EFFICACY.—Flower visitors effecting pollination were observed and collected whenever possible. Details of floral adaptations for pollination, flower phenology, and pollinator behavior were recorded for individual species (table 1). The Re-

productive Efficacy, here defined as reproductive output under maximal conditions of pollination, was determined for a number of the species studied (table 8) by comparing percent fruit set under controlled

cross-pollination (in the incompatible and dioecious species) or following automatic selfing (in the case of highly autogamous self-compatible species) with open pollination fruit set, which was estimated by

TABLE I. Life forms, floral morphology, flowering season and pollinators of species of a secondary deciduous tropical forest.

Species and life form	Floral morphology	Flowering season	Pollinators ¹
TREES			
<i>Acacia macracantha</i> H&B (LEGUMINOSAE: MIMOSOIDEAE)	andromonoecious	mid wet	Apidae: <i>Trigona testaceicornis</i> (Lep). Chalcididae: <i>Metadontia</i> sp. Syrphidae: <i>Allograpta</i> sp.
<i>Bursera simaruba</i> (L.) Sarg. (BURSERACEAE)	dioecious	start wet	wind
<i>Calliandra laxa</i> Benth. (LEGUMINOSAE: MIMOSOIDEAE)	andromonoecious	end dry	bees
<i>Capparis flexuosa</i> L. (CAPPARIDACEAE)	hermaphrodite	end dry	Anthophoridae: <i>Xylocopa virescens</i> Lep. Scoliidae: <i>Campsomeris servilled</i> (G-M)
<i>Erythroxylum bauanense</i> Jacq. (ERYTHROXYLACEAE)	distylous	start wet	bees
<i>Guazuma tomentosa</i> HBK (STERCULIACEAE)	hermaphrodite	start wet	bees
<i>Guettarda roupalaefolia</i> Rusby (RUBIACEAE)	distylous	mid wet	butterflies, moths
<i>Prockia flava</i> Karst. (FLACOURTIACEAE)	hermaphrodite	mid wet	Apidae: <i>Apis mellifera</i> L. <i>Bombus koblii</i> Ckll.
<i>Randia dioica</i> Karst. (RUBIACEAE)	dioecious	start wet	nocturnal moths
<i>Sorocea sprucei</i> (Baill.) Karst. (MORACEAE)	dioecious	start wet	wind
<i>Tabebuia spectabilis</i> Planch. (BIGNONIACEAE)	hermaphrodite	end dry	Apidae: <i>Bombus koblii</i> Ckll.
<i>Zanthoxylum ciliata</i> Engl. (RUTACEAE)	dioecious	mid wet	bees
<i>Ximania americana</i> L. (OLACACEAE)	hermaphrodite	end dry	bees
SHRUBS			
<i>Bredemeyera floribunda</i> Willd. (POLYGALACEAE)	hermaphrodite	end wet	bees
<i>Capparis verrucosa</i> Jacq. (CAPPARIDACEAE)	hermaphrodite	end dry	Apidae: <i>Bombus koblii</i> Ckll.
<i>Eugenia</i> sp. (MYRTACEAE)	hermaphrodite	start wet	Apidae: <i>Trigona testaceicornis</i> (Lep.) <i>Apis mellifera</i> L. Halictidae: <i>Augochloropsis</i> affin. <i>fulvofimbriata</i> (Fr.)
<i>Zanthoxylum pterota</i> L. (RUTACEAE)	hermaphrodite	end dry	not collected
VINES			
<i>Banisteriopsis muricata</i> (Cav.) Cuatr. (MALPIGHIACEAE)	hermaphrodite	end wet	bees
<i>Securidaca scandens</i> Jacq. (POLYGALACEAE)	hermaphrodite	start wet	Apidae: <i>Bombus koblii</i> Ckll. hummingbirds
<i>Urvillea ulmacea</i> HBK (SAPINDACEAE)	andromonoecious	mid wet	bees
HEMIPARASITES			
<i>Phibirusa aduna</i> (Meyer) Maguire (LORANTHACEAE)	gynodioecious	start wet	Apidae: <i>Trigona testaceicornis</i> (Lep.) <i>Apis mellifera</i> L.
<i>Phibirusa</i> sp. 2 (LORANTHACEAE)	hermaphrodite	end wet	bees

¹ We have been unable to obtain determinations on the un-named insects.

previously tagging flowers and later observing the percentage forming fruits. This measure of reproductive efficacy estimates seed set under maximal conditions of pollination and not the potential seed set in terms of flower production. It therefore also provides a direct indication, in the case of outbred

species, of pollinator efficiency. Under obligate outbreeding the reproductive efficacy measures the percentage of flowers that have been successfully cross-pollinated. For a generically self-compatible species capable of some degree of autogamy it estimates natural cross-pollination, geitonogamous and auto-

TABLE 2. Results of controlled self- and cross-pollination and self-incompatibility indices for hermaphrodite and dioecious species with hermaphrodite individuals or flowers.

Species	Individuals		Flowers		Percent fruits		Average seed/ flower crossed		ISI Index	Con- clusion ³
	Selfed	Crossed	Selfed	Crossed	Selfed	Crossed	Selfed	Crossed		
TREES										
<i>Acacia macracantha</i>	7	6	15,780	3,786	0	0.19	0	0.02	0	SI
<i>Calliandra laxa</i>	6	5	139	136	0	11.76	0	0.37	0	SI
<i>Capparis flexuosa</i>	5	5	86	25	10.46	16.00	0.15	0.40	0.37	SC
<i>Erythroxylum havanense</i>										
Short-styled	1	NA ¹	7	NA ²	0	NA	0	NA	0	SI
Long-styled	1	NA	57	NA	0	NA	0	NA	0	SI
<i>Guazuma tomentosa</i>	3	3	223	128	0	28.12	0	NA	0	SI
<i>Guettarda roupalaefolia</i>										
Short-styled	7	2	22	35	0	0.14	0	0.37	0	SI
Long-styled	3	4	30	51	3.33	0.98	0.13	0.13	1	SC
<i>Prockia flava</i>	3	3	62	46	9.67	54.34	1.24	21.27	0.16	SI
<i>Tabebuia spectabilis</i>	2	1	97	32	0	9.37	0	16.58	0	SI
<i>Ximenesia americana</i>	7	2	334	10	0	40.00	0	0.40	0	SI
SHRUBS										
<i>Bredemeyera floribunda</i>	7	7	831	899	0	50.05	0	0.60	0	SI
<i>Capparis verrucosa</i>	6	6	40	41	15.00	31.07	0.35	3.73	0.09	SI
<i>Eugenia</i> sp.	2	NA	51	NA	0	NA	0	NA	0	SI
VINES										
<i>Banisteriopsis muricata</i>	8	5	434	195	0.99	0.23	0.03	0.13	0.26	SC
<i>Securidaca scandens</i>	11	9	454	33	13.43	21.21	0.13	21.12	0.63	SC
<i>Urvillea ulmacea</i>	1	5	32	294	0	54.24	0	0.71	0	SI

¹ Cross data destroyed by outside interference.

² The 'selfs' include Long x Long and Short x Short and well as Long selfed and Short selfed, respectively.

³ Two additional species were tested for automatic selfing only; 42.15 percent of 539 flowers of *Zanthoxylum pterota* and 26.05 percent of 255 flowers of *Phthirusa* sp. 2 set fruit upon automatic selfing, these species thus probably being both genetically self-compatible and autogamous.

TABLE 3. Automatic selfing indices for self-compatible hermaphrodites.

Species	Ind.	Automatic selfing			Controlled ¹ selfing	Automatic selfing index (IAS)
		Flowers	Percent flowers forming fruits	Average seed per fruit	Percent flowers forming fruits	
<i>Banisteriopsis muricata</i>	8	1,273	0	0	2.99	0
<i>Capparis flexuosa</i>	7	322	3.72	1.33	10.46	0.35
<i>Capparis verrucosa</i>	3	119	4.20	2.40	15.00	0.28
<i>Prockia flava</i>	3	38	0	0	9.76	0
<i>Securidaca scandens</i>	11	454	13.44	1.00	1.00	1.00

¹ Number of individuals and flowers hand-selfed reported in table 2.

TABLE 4. Relative seed set per fruit following controlled self- and cross-pollination in self-compatible hermaphrodites.

Species	Selfed		Crossed		Relative number seeds per fruit
	Flowers pollinated	Seeds/fruit	Flowers pollinated	Seeds/fruit	
<i>Capparis flexuosa</i>	86	1.44	25	2.50	0.57
<i>Capparis verrucosa</i>	40	2.33	41	11.77	0.19
<i>Prockia flava</i>	62	12.83	46	39.96	0.32
<i>Banisteriopsis muricata</i>	434	1.15	195	1.38	0.83
<i>Securidaca scandens</i>	454	1.00	33	1.00	1.00

TABLE 5. Results of controlled self- and cross-pollination in the morphologically gynodioecious *Phthirusa aduna* (LORANTHACEAE).

	Individuals	Flowers crossed	Percent fruits formed	Seeds per flower crossed
Hermaphrodites selfed	4	397	0	0
Hermaphrodites crossed	5	45	0	0
Female x hermaphrodite ¹	7	8	37.5	0.65

¹ Pollen parent

matic selfing, while for non-autogamous self-compatible species it estimates open cross-pollination and geitonogamous selfing.

POPULATION AND REPRODUCTIVE DENSITY.

—Intraspecific population density and reproductive density were determined in order to assess the effect of population density on inter-plant pollinator movement. Total population density (for plants exceeding 50 cm in height) was determined by counting the number of individuals on the entire site (for species represented by few individuals), or by sampling 20 randomly located 5 m x 5 m quadrats. All hemiparasites were counted. Reproductive density was based on counts of all flowering individuals per species during 1975-76. Densities are expressed in terms of number of individuals per hectare (table 7).

RESULTS

BREEDING SYSTEMS.—None of the species investigated proved to be apomictic. Ten species (45.55%), including trees, shrubs, and vines, possess genetic self-incompatibility (table 2). Two of these (*Guetarda roupalaeifolia* and *Erythroxylum havanense*) are distylous and thus heteromorphically self-incompatible. One of three long-styled plants of *G. roupalaeifolia* set seed both on selfing and crossing to other long-styled individuals. However, intra-flower selfing is largely prevented by the relative position of the stigmas and anthers.

The andromonoecious *Urvillea ulmacea* is both genetically self-incompatible and functionally unisexual. Since the otherwise fully fertile anthers fail to dehisce, the hermaphrodite flowers are functionally pistillate. Additionally, pistillate and staminate flowers open in sequential blocks along the inflorescence. Staminate flowers appear initially for 7-16 days, followed by pistillate flowers for 5-7 days. For the final two weeks of anthesis only staminate flowers are produced. As individual flowers persist for less than a day and sexuality is highly synchronized over the entire plant, the populations are functionally dioecious. Simultaneous anthesis by pistillate and staminate flowers in the same inflorescence was observed in only one individual of the entire population. Reports of self-incompatibility in the families Olacaceae and Polygalaceae seem new.

The self-incompatibility indices of seven hermaphroditic species (table 2) exceeded zero. The level of self-compatibility in *Prockia flava* and *Capparis verrucosa* (ISI = 0.06 and 0.09, respectively) is low. *Banisteriopsis muricata*, *Capparis flexuosa*, *Zanthoxylum pterota*, and *Phthirusa* sp. 2 are moderately self-compatible. *Securidaca scandens* is highly self-compatible. The incomplete compatibility of all these species is determined by lower average seed number per fruit combined with fewer self-pollinated flowers setting fruits (table 4). Intrinsic and extrinsic factors affecting stigma maturity, which in turn may affect the percentage of successfully pollinated stigmas, should be the same in controlled self- and cross-pollinations. Yet a higher proportion of

flowers failed to set fruit and seed following the selfing of all self-compatible species. This finding indicates that while some of a plant's flowers are functionally self-compatible, others are functionally self-incompatible, and the border between self-compatibility and self-incompatibility is a highly labile one. Complete self-incompatibility, however, was not encountered in any individuals of species exhibiting self-compatibility.

The level of adaptation for autogamy is highly variable among generically self-compatible species (table 3). In *Prockia flava* and *Banisteriopsis muricata*, isolation of stigmas and anthers combined with dichogamy is sufficient to restrict entirely intra-flower autogamy. However, a certain amount of inter-flower geitonogamous selfing must occur in both species. The actual quantity of geitonogamously selfed seeds produced by *Prockia flava*, given its very low ISI, will be minimal. In the moderately self-compatible *B. muricata* approximately four intra-individual pollen transfers will yield the same quantity of seed resulting from one inter-plant cross-pollination. Mechanical selfing on a moderate scale is permissible in *Capparis flexuosa* and *C. verrucosa*. Despite its relatively high selfing capacity, given its very low level of self-compatibility, the actual quantity of seed resulting from selfing in *C. verrucosa* will be negligible. In *C. flexuosa*, on the other hand, geitonogamy combined with automatic selfing could yield as high as 12 percent of the maximal seed set expected under 100 percent outcrossing.

Securidaca scandens and *Phthirusa* sp. 2 are highly adapted for autogamy. The flowers of the latter are cleistogamous, while pollen is directly deposited on the receptive stigma in the former. The red, showy flowers of *S. scandens* are visited abundantly by bees and hummingbirds. As the hummingbirds forage on several plants the species probably enjoys considerable outcrossing.

The ISI in *Prockia flava* and in *Capparis ver-*

rucosa is so low that these species may be considered essentially incompatible. The total percentage of incompatible species thus is 54.45 (table 6). Considering these together with the truly dioecious *Sorocea sprucei*, *Randia dioica*, and *Zanthoxylum ciliata*, and the functionally dioecious, but morphologically gynodioecious (table 5) *Phthirusa aduna* (cf. Arroyo and Raven 1975), 77.17 percent of the species in the sample are obligately adapted for outbreeding and thus are totally dependent upon inter-plant pollen transference.

POPULATION AND REPRODUCTIVE DENSITY.—Population density (table 7) is highly variable among the species studied and probably reflects the changing roles of the constituent species in the process of succession. In the trees the average number of individuals per hectare ranges from a low of 3.5 in *Bursera simaruba* to an all-community-high of 1198.2 in *Erythroxylum havanense*. Shrub (7.0-224.9 individuals per hectare) and vine and hemiparasite (9.9-524.9 individuals per hectare) densities are equally variable. The average tree density (307.5 individuals per hectare) is not statistically different from the average shrub density (101.6 individuals per hectare) ($t_{12} = 0.079$; NS at the 0.05% level). The average density of vine and hemiparasite species (258.5 individuals per hectare) is significantly higher than both the average tree ($t_{12} = 1.16$, significant at the 0.05% level) and shrub ($t_8 = 8.53$; significant at the 0.01% level) densities.

Less variation exists among the densities of reproductively mature individuals. Among the trees, excluding the overwhelmingly common *Erythroxylum havanense* (r.d. = 165.9 individuals per hectare), reproductive density varies from 3.1 to 19.9 individuals per hectare. The overall average tree reproductive density of 19.3 individuals per hectare is not significantly different from the overall shrub reproductive density ($t_{15} = 0.050$; NS at the 0.05% level). However, the mean reproductive density of vines and hemiparasites greatly exceeds that of both shrubs and trees ($t_8 = 8.53$ for shrubs and $t_{15} = 10.14$ for trees; both significantly different at the 0.01% level).

The relationship between the percentage of individuals per species that have reached reproductive maturity and the total number of individuals per species, per unit area (table 7) provides an interesting insight into the ecological dynamics of the community. In species represented by low numbers of individuals, the proportion of the population that has reached reproductive maturity is invariably high. In contrast, where large number of individuals predominate, there are few reproductively mature in-

TABLE 6. Relative percentages of different breeding systems represented in the secondary deciduous tropical forest.

Breeding system	Number of species	Percentage of total
Self-incompatible	12	54.45
Self-compatible		
Autogamous	2	9.09
Non-autogamous	3	13.63
Dioecious and functionally dioecious	5	22.72
Total species obligately outbred	17	77.17

TABLE 7. Total population and reproductive densities.

Species and life forms	Total individuals per hectare ¹	Reproductive individuals per hectare	Percent of total reproductively mature
TREES			
<i>Acacia macracantha</i>	NA ²	9.9	NA
<i>Bursera simaruba</i>	NA	3.5	NA
<i>Calliandra laxa</i>	549.8	5.0	0.90
<i>Capparis flexuosa</i>	374.9	19.9	5.79
<i>Erythroxylum havanense</i>	1198.2	165.9	13.85
<i>Guazuma tomentosa</i>	5.0	5.0	100.00
<i>Guettarda roupalaefolia</i>	274.9	5.5	1.99
<i>Prockia flava</i>	4.5	3.1	70.16
<i>Randia dioica</i>	NA	5.0	NA
<i>Sorocea sprucei</i>	99.9	5.0	4.96
<i>Tabebuia spectabilis</i>	4.4	3.5	77.70
<i>Zanthoxylum ciliata</i>	549.9	13.9	2.52
<i>Ximения americana</i>	13.5	6.0	43.97
MEANS (SD)	307.49 (346.50)	19.32 (41.01)	32.18 (37.70)
SHRUBS			
<i>Bredemeyera floribunda</i>	224.8	7.5	3.33
<i>Capparis verrucosa</i>	7.0	4.0	57.10
<i>Eugenia</i> sp.	49.7	2.0	4.02
<i>Zanthoxylum pterota</i>	124.9	5.0	4.00
MEANS (SD)	101.62 (72.01)	4.62 (1.77)	17.11 (26.66)
VINES AND HEMIPARASITES			
<i>Banisteriopsis muricata</i>	274.4	10.0	4.04
<i>Securidaca scandens</i>	524.9	NA	NA
<i>Urvillea ulmacea</i>	NA	10.0	NA
<i>Phthirusa aduna</i>	224.9	10.0	4.44
<i>Phthirusa</i> sp. 2	9.9	4.0	40.12
MEANS	258.5 (163.80)	8.5 (2.32)	16.2 (20.71)

¹ Plants exceeding 50 cm height, except in the cases of hemiparasites where all individuals were counted.

² NA: data not available.

dividuals. In *Guazuma tomentosa* (5 ind./ha) all individuals are of reproductive age. This relationship indicates that certain species of the community are undergoing little (e.g. *Capparis verrucosa*, *Ximения americana*, *Phthirusa* sp. 2) or essentially no regeneration (e.g. *Tabebuia spectabilis*, *Prockia flava*, *Guazuma tomentosa*), whereas a second group of species (e.g. *Calliandra laxa*, *Guettarda roupalaefolia*, and *Bredemeyera floribunda*) appear to be regenerating abundantly. The first species are probably being replaced by other species, whereas those of the second group appear to be increasing in abundance as the community matures.

REPRODUCTIVE EFFICACY.—All species studied set seed under natural conditions. No clear distinction exists between the reproductive efficacy of self-compatible species and those obligately adapted for

outbreeding ($t_8 = 0.010$; NS at the 0.05% level), nor between self-compatible and self-incompatible hermaphrodite species ($t_7 = 0.044$; NS at the 0.05% level). However, the functionally dioecious *Phthirusa aduna* produces a much higher proportion of seed than do other self-incompatible species. Bawa and Opler (1975) observed a general tendency for higher seed set in dioecious species in a tropical deciduous forest in Costa Rica. They suggested that the deposition of incompatible pollen grains on the stigmas of a self-incompatible species, by way of geitonogamy, might, due to spatial considerations on the stigma itself, lower the probability with which compatible grains would germinate and reach the ovary. Recently Heslop-Harrison (1975) demonstrated callose production on the stigma as part of the incompatibility reaction. Howlett *et al.* (1975) found a depression in seed set when compatible pollen grains were mixed

TABLE 8. Reproductive efficacy of some species of a secondary deciduous tropical forest.

Species	Natural pollination			Cross-pollination			Reproductive efficacy
	Individuals	Flowers pollinated	Percent flowers forming fruits	Individuals	Flowers pollinated	Percent flowers forming fruits	
SELF-COMPATIBLE SPECIES							
<i>Banisteriopsis muricata</i>	7	2,069	0.24	5	194	9.23	0.03
<i>Capparis flexuosa</i>	4	336	4.76	5	25	16.00	0.29
<i>Securidaca scandens</i>	10	947	35.27	9	33	21.21	1.66 ¹
MEANS (SD)							0.66 (0.87)
SELF-INCOMPATIBLE SPECIES							
<i>Bredemeyera floribunda</i>	6	5,056	5.70	7	899	36.26	0.16
<i>Calliandra lasca</i>	4	135	3.70	5	135	11.76	0.31
<i>Capparis verrucosa</i>	2	22	18.18	6	41	31.70	0.57
<i>Tabebuia spectabilis</i>	2	118	4.35	1	32	9.27	0.47
<i>Urvillea ulmacea</i>	5	431	23.66	5	294	54.42	0.43
<i>Ximenesia americana</i>	3	415	10.00	2	10	40.00	0.25
MEANS (SD)							0.36 (0.15)
DIOECIOUS SPECIES							
<i>Phibirusa aduna</i>	28	1,301	65.26	7	9	37.50	1.90
MEAN (SD) all obligately outbred species							0.58 (0.59)

¹ Values exceeding 1 are possibly due to repeated instances of pollination under natural conditions, which in turn would ensure a greater probability that a stigma is pollinated in the receptive condition.

with and applied to the stigma with incompatible grains. A reverse effect, that is stimulation of self-fertilization, was observed to some extent when wall components (bearing the self-incompatibility substances) of self-compatible grains were mixed with incompatible pollen. These recent findings might be important in the light of observed differences in the seed set of dioecious and genetically self-incompatible species. The pollen borne on stigmas of pistillate dioecious plants will always be totally compatible; however, as a greater proportion of the pollen transfers in self-incompatible hermaphrodites results from intra-plant pollinator movement, an individual stigma will bear a high proportion of incompatible grains. Notwithstanding some compensation through the stimulation of self-fertilization by comparable grains, the lowered fecundity of self-incompatible hermaphrodites as compared with dioecious species might be due to the inhibitory effect of an excess of incompatible grains. There are striking differences among the reproductive efficacies of the self-compatible species *Securidaca scandens*, *Capparis verrucosa*, and *Banisteriopsis muricata*. The high reproductive efficacy of the first is due to its capacity for autogamy. Causes for the lower reproductive efficacies of *B. muricata* and *C. verrucosa* are less clear.

Reproductive efficacy and pollination efficiency

have rarely been estimated on a community basis. Percival (1974) assessed proportions of stigmas carrying pollen for several species in tropical scrub in Jamaica. Well over 50 percent of the stigmas bore pollen in almost all species, and 100 percent of the stigmas were pollinated in many. These measurements, while providing an estimate of pollinator movement, cannot be directly compared with pollinator efficiency based on seed set, since in self-incompatible species a large proportion of the stigmas perhaps bear only incompatible grains, not capable of fertilizing the ovaries of the flowers upon which they occurred. Bawa (1974) provided data on fruit set under natural conditions and following controlled cross-pollination for a Costa Rican deciduous tropical forest. Using the data, reproductive efficacy as described in this study may be computed. A third of the species in the Costa Rican forest have reproductive efficacies lower than 0.1. The average reproductive efficacy for self-compatible species (0.67) is similar to the value of 0.66 that we obtained for self-compatible species. However, the values for self-incompatible species (0.16), and for all species taken together (0.24) fall significantly below the values of 0.36 and 0.61 that were obtained in Venezuelan forest. On the average, species of secondary deciduous forest (our study) appear to demonstrate a higher

reproductive efficacy than do species of more mature semi-deciduous forest.

DISCUSSION

The predominant reproductive strategy among plants of the secondary tropical forest is obligate outbreeding, either through self-incompatibility mechanisms, dioecy or various forms of functional dioecy. The proportion of obligately outbreeding species (77.17%) is remarkably similar to the 76 percent outbred species registered in a primary, but disturbed, lowland forest in Costa Rica (Bawa 1974). The relative proportions of self-incompatible and dioecious species in the two communities are also similar. Among the self-compatible species in the secondary deciduous forest, only two are likely to undergo extensive autogamy; all others are visited by pollen vectors and in fact depend upon animal-mediated pollen transfer for seed set, whether via cross-fertilization or self-fertilization. Among this same group of self-compatible species, the low seed set following self-pollination as compared with cross-pollination is possibly due to exposure of lethal zygotic recessives, a phenomenon not uncommon in self-compatible, but predominantly outcrossed trees (Hagman 1967). This possibility lends further support to the contention that such self-compatible plants are largely outcrossed.

Andromonoecy is characteristic of three species which have also been demonstrated to possess self-incompatibility. Remnants of bisexuality in the flowers of the andromonoecious species suggest that hermaphroditism preceded dicliny. While the latter may promote outcrossing in self-compatible species (Lloyd 1972), it can be of little adaptive value in this respect in a self-incompatible species. In the present situation we are inclined to believe that andromonoecy and functional monoecy are strategies that determine a more efficient use of reproductive energy. In andromonoecious species the entire inflorescence functions as the unit of pollinator attraction. The proportion of pistillate or hermaphrodite flowers that actually mature fruit, however, due to post-fertilization competition between recently pollinated ovules, is very low. Female sterility in a large part of an inflorescence prevents unnecessary outlay of energy for initial fruit development, a large part of which cannot be matured. On the other hand, failure of anther dehiscence in morphologically hermaphrodite flowers of *Urvillea*, combined with dichogamy, further streamlines reproductive energy usage by eliminating pollen loss through geitonogamy, and, in fact, as was suggested earlier, may enhance

the probability that all ovules will be fertilized.

Various authors have stressed that self-comparability may have been favored in tropical ecosystems. The basis for these arguments is either low population density of the component species (Corner 1954, Fedorov 1966) or a combination of the latter and structural complexity (Baker 1959). That population density is not a limiting factor for obligate outbreeding in secondary deciduous tropical forest is evidenced by the high proportion of obligately outbreeding species and the relatively high reproductive efficacies demonstrated. Certain species are apparently being replaced due to seral progression. While failure of seed set due to inadequate pollination could be a contributory factor in the regulation of successional changes, it appears not to be so in this particular community. An important consideration in evaluating our results in relation to tropical ecosystems in general is the relatively low species-richness of the secondary community, which is considerably less species-rich than climax tropical vegetation. Richards (1952) reports 70-91 species of trees on 1.5 ha plots for several mixed tropical rainforests. Black *et al.* (1950) registered 41-79 tree species on 1 ha virgin Brazilian rainforest plots, while Smith (1970) estimated a total of 230 species (all life-forms included) on a 2 ha plot of virgin rainforest in Puerto Rico. These figures greatly exceed the 93 species collected on the 2 ha plot of secondary deciduous forest. Although reproductive density data are unavailable for other types of tropical vegetation, it may be assumed that the number of reproductively mature individuals per species is higher in secondary vegetation. As some indication of this, Black (1950) recorded a median tree species density of two individuals (over 50 cm DBH) per hectare on 1 ha plots of Brazilian rainforest, whereas we found the median reproductive density for trees to be 5/ha, with no species represented by fewer than 3.5/ha. As comparative data become available, the population density of species in early successional tropical communities may prove to be very similar to if not exceeded by that of species in certain relatively speciose, temperate xeromorphic communities in Austria (Parsons and Cameron 1974) and South Africa (Richards 1969).

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