

THE SEXUALITY OF THE
BARRO COLORADO ISLAND FLORA (PANAMA)

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The sexual expression of species making up a flora have frequently been analyzed, but as yet no enumeration has been given for any entire neotropical flora. Probably the most thorough survey of the distribution of sexual expression was that made by Yampolsky and Yampolsky (1922), but that now much out of date survey was made on a worldwide phyllogenetic basis rather than on a geographical basis. The recent completion of the Flora of Barro Colorado Island (Croat, 1978) affords the opportunity to report on the sexual behavior of a species-rich tropical forest in the isthmus of Panama. Barro Colorado Island, which lies in Gatun Lake midway between the Atlantic and Pacific Oceans, has a flora of 1,369 species of vascular plants. Although the area is small in size (ca 6 square miles), it is representative of tropical moist forest, which makes up approximately 50% of the total area of Panama. Moreover, it occupies a central position between North and South America and apparently has acquired nearly equal numbers of species from the Central and South American floras (Croat and Busey, 1975).

Of the 1,212 species of native phanerogams in the flora, 286 (24%) have unisexual flowers. Of these, 106 (9%) are dioecious, 132 (11%) are monoecious, (4 are monoecious or dioecious and are included in both categories), and 52 (4%) are polygamous.

On BCI there are 481 arborescent species (39.7% of the native vascular flora) (See Table 1). Of this number, 34 (6.4%) are trees which may be larger than 30 m and are possible emergents, while 177 (37%) are trees 10-30 m tall. The two groups inclusively are referred to here as medium to large trees. There are 265 climbing plants making up 20% of the flora and 466 herbaceous plants (not counting herbaceous vines) accounting for 35.5% of the phanerogamic flora.

METHODS

Field work was carried out on Barro Colorado Island during the years 1967 through 1975. Plants were observed for obvious signs of sexual dimorphism and were designated as dioecious, monoecious and polygamous on this basis. Species in certain families, such as Meliaceae and Burseraceae where others have reported dioecism, were examined in greater detail but no controlled experiments were carried out. Though no apparent sexual dimorphism was observed in the flowers of some members of these families, they were presumed dioecious because during a normal flowering season some individuals set abundant fruit while others did not set fruit. Examples of such species are Protium panamense (Burseraceae) and Guarea glabra (Meliaceae). All other members of the Burseraceae and Meliaceae which are considered dioecious here are the result of reports by other workers (Styles, 1972; Bawa & Opler, 1975). With these exceptions all dioecious species reported here are based on obvious and conspicuous sexual dimorphism in the flowers.

Monoecious species and polygamous species are all reported on the basis of obvious sexual dimorphism in the flowers. Flowers of the Sapindaceae are however suspect owing to studies by Bawa (1977) (See the discussion under polygamous species). All Cucurbitaceae, though initially believed to be dioecious, are placed among the monoecious species based on observations by Bawa (personal communication).

MONOECISM (Tables 1 and 5)

A total of 132 (11%) of the native species on Barro Colorado Island are monoecious (Table 5). This compares very closely to the 10% reported by Bawa and Opler (1975) for the Comelco area of Guanacaste, Costa Rica. However, their study was limited to tree species while this study has dealt with the entire phanerogamic flora.

Monoecious species are most common percentage-wise among medium to large trees but a smaller percentage of these trees are monoecious (15%)

than are dioecious (21%). The same is true of climbing plants, 12% are monoecious versus 8% dioecious, but the differences are not significant. A significantly higher percentage of herbaceous species are monoecious, however, with 11% monoecious herbs versus only 2% dioecious herbs. Of the small trees and shrubs, 7% are monoecious and 12% are dioecious.

POLYGAMOUS SPECIES (Table 1 and 6)

The polygamous conditions of sexuality where both unisexual (usually staminate) and hermaphroditic flowers are present on the same or different individuals of a species is the most difficult sexual condition to classify, owing to the variety of sexual states which may be present and the difficulty of ascertaining whether certain sexual structures are functional. For example, while Sapindaceae usually are polygamous and their bisexual flowers appear to have both sexes functional, Bawa (1977) has shown the anthers of bisexual flowers of Cupania guatemalensis to be nonfunctional, apparently never opening. He concludes that perhaps this is true of other polygamous species in the family as well. Lacking more evidence to indicate that such is true for all polygamous species, I am including here as polygamous all species which have both functional hermaphroditic flowers as well as unisexual flowers.

Polygamous species (52) are found in relatively few (9) families and are most abundant in Compositae and Sapindaceae, the latter being a family principally of lianas.

DIOECISM (Tables 1 and 7)

Arborescent Species

The medium to large trees on BCI are 21% dioecious. The dioecious condition of a number of BCI species has not been verified, and their presence on the list of dioecious species is based on studies by other workers (Styles, 1972; Bawa and Opler, 1975). These include most species of Burseraceae, Polygonaceae, and Meliaceae which occur on the list though observation on

Guarea glabra Vahl (Meliaceae) and Protium panamense (Rose) I.M. Johnston (Burseraceae) indicate that they are dioecious. (See comments about these species under Methods). On the other hand, a number of additional species may ultimately be added to the list, such as other poorly known species of Pouteria (Sapotaceae).

Bawa and Opler (1975) reported that 22% of the trees from the Comelco study area in Guanacaste, Costa Rica, were dioecious while only 11% of the shrubs were dioecious. Comparable figures for BCI are 21% dioecious species for trees and 12% dioecious species for shrubs and small trees. Bawa and Opler's list of dioecious species (p.168) agrees in general with my size class of medium to large trees (trees more than 10 m tall) but some of these taxa fall into my small tree and shrub category (K. Bawa, pers. comm.). These include 2 species of Randia, Allophylus occidentalis, Xylosma sp. and Margaritaria nobilis. If only trees more than 10 m tall are considered, the percentage of dioecious species is 19% in the Comelco region, slightly lower than on BCI.

The category small trees and shrubs on BCI is much larger than the category medium to large trees, but contains proportionally fewer dioecious species. For example, on BCI, there are 270 species of shrubs or small trees (less than 10 m tall). This includes the 16 hemiepiphytic shrubs and the 7 parasitic shrubs (3 of which have unisexual flowers). If the shrubs or small trees category is considered alone, 12% of their species are dioecious while shrubs considered alone have 4% (4 of 93) of their species dioecious.

The more restricted category for trees (i.e., those more than 10 m tall) yielding 21% dioecious species also corresponds rather well to reports for tropical floras elsewhere, e.g., 27% for South Florida (Tomlinson, 1974) and 26%* for a dipterocarp forest of Sarawak (Ashton, 1969), but falls

* Ashton (1969) included in his count some protandrous and some protogynous, hermaphroditic species.

far short of the percentages of dioecious species of trees calculated by Bawa and Opler (1975) for species reported by Jones (1955) for a rain forest in Nigeria (38-40%).

It would be interesting to make direct comparisons between the sexual expression of the tropical dry forest of Costa Rica and that of the tropical moist forest area of Panama. However, no such comparisons can be made, owing in part to the reasons discussed above. In addition to possible differences in our respective classification of trees, there are actual differences in which species I have considered dioecious. For example, I have considered as hermaphroditic, monoecious or polygamous, some taxa which Bawa and Opler have considered dioecious, e.g., Spondias, Genipa, and most Sapindaceae (Tables 5-7). Actually it is very difficult to clearly separate species into distinct classes based on their sexual expression since the degree to which a species is hermaphroditic or unisexual is variable. For example, some families with polygamous flowers, such as the Sapindaceae, have bisexual and pistillate flowers in varying proportions. Some polygamous species have such a preponderance of pistillate flowers that they can be said to be functionally pistillate. While most Serjania species are polygamous, one species, S. cornigera, may be found to vary from year to year or even during the course of a single growing season. Lee (1967) has found that tendencies for maleness or femaleness in Swietenia (Meliaceae) may vary from year to year. Bawa (1977) indicates the same tendency in Cupania (Sapindaceae). In this case trees which produced only staminate flowers one year still bore fruits from the previous year. Other species reported by Bawa (1974) to be variable in their sexual expression in a local area include Simaruba glauca, Allophylus occidentalis and Coccoloba spp. Klæhn (1961), working with temperate trees, cites examples of similar differences in sexual tendencies from tree to tree in the same population. Styles (1972) states that in Meliaceae the proportion of staminate to pistillate or hermaphroditic to unisexual flowers is phenologically variable within a single flowering season. I have observed the same phenomenon on other taxa, such as Trichospermum

(Tiliaceae). Even completely hermaphroditic species may be so prominently protogynous or protandrous as to be functionally unisexual at any point in time. Bawa (1977) has found sexual expression in Cupania (Sapindaceae) to shift from staminate to pistillate and back to staminate in a single flowering season. The occurrences of such sexual intergradations increases the complexity of studying sexual expression in the tropics.

As Bawa and Opler (1975) pointed out, it is often very difficult to distinguish dioecious species from hermaphroditic species. This is particularly true in such families as Meliaceae, Burseraceae, Sapindaceae, and Anacardiaceae. Many dioecious members of these families can only be distinguished as dioecious by repeated observation of flowering and degree of fruit set or alternatively by pollination experimentation. Styles (1972) found minute but consistent differences in some genera of Meliaceae but no differences whatever in other genera even though experimentation has shown them to be dioecious or monoecious. In addition to the variation in sexual expression at the populational level, there is the possibility of a clinal variation in sexual expression over the extent of the species' range.

I suspect that within some species there is intraspecific variation extending from individuals which are functionally hermaphroditic to those which are functionally staminate or pistillate. For example, while Spondias radlkoferi Donn. Sm. (S. nigrescens Pittier) (Anacardiaceae) is dioecious in Guanacaste, it is preponderately hermaphroditic in central Panama. All plants have very large numbers of hermaphroditic flowers and a small number of pistillate flowers and all individuals observed set fruit after flowering.

Scandent and Herbaceous Species

More interesting than the comparison of percentages of dioecious trees and shrubs is the percentage of scandent dioecious species for BCI as compared to the Comelco study site. Bawa and Opler (1975) emphasized forest trees as being characteristic of dioecism and reported that there

were no dioecious vines or lianas in the Guanacaste study site. Despite the fact that larger trees remain the most important for dioecism, 20% of the dioecious species on BCI are vines or lianas. Representatives include Gnetaceae (1 sp.), Dioscoreaceae (5 spp.), Menispermaceae (7 spp.) Polygonaceae (1 sp.), Smilacaceae (5 spp.), Urticaceae (1 sp.), and Nyctaginaceae (1 sp., Pisonia, considered a tree by Bawa and Opler).

While there are no herbaceous plants in Guanacaste which were reported to be dioecious, there are 8 herbaceous species on BCI which are dioecious. (Subsequent to publication of these figures for Guanacaste, the authors have discovered 6 or 7 species of Dioscorea at the Comelco study sites (Paul Opler, pers. comm.).)

MORPHOLOGICAL FEATURES OF DIOECIOUS SPECIES

The dioecious species on Barro Colorado Island were studied to test the statements made by Bawa and Opler (1975) concerning the morphology of dioecious species. These were the following:

1. That dioecious species often display sexual dimorphism in flower size with the pistillate flowers being larger than their staminate counterparts.
2. That flowers of dioecious species are generally not colorful or showy, usually being white to yellow or pale green.
3. That dioecious species often have flowers substantially smaller than congeneric hermaphroditic species.

1. Of the 106 dioecious species on BCI, 97 were studied for length of staminate flowers (Table 2; Figures 1 and 2). Flower measurements are those presented in the Flora of Barro Colorado Island (Croat, 1978). Only the length of the flower is considered except where the width was noticeably greater than the length. In such cases, the width of the flower was used. The measurement used was the upper limit of normal variation, but not the

unusual higher variant appearing in parenthesis, e.g., 10-12(15) mm, the parenthesized measurement referring to fewer than 5% of the cases or to reports of lengths for the same species growing elsewhere. The structures measured were the tepals, petals or sepals (depending on which were longer) except for flowers without petals or with a very reduced perianth. In such cases, the length of the sexual parts, i.e., stamens or pistil, was used. The average length of staminate flowers was 7.6 mm (Table 2). The standard error, however, of 20.1 is large because of a few species with large and very large flowers. If flowers 1 cm or more long are excluded from consideration, the average flower size for dioecious staminate flowers is 3.16 mm. Dioecious species with flowers 1 cm or more long had an average staminate flower size of 30.1 mm. There are 16 species in this latter category: Carica, Jacaratia (Caricaceae), Diospyros (Ebenaceae), Clusia, Tovomita (2 spp.) (Guttiferae), Hampea (Malvaceae), Guarea (2 spp.) (Meliaceae), Neea (Nyctaginaceae), Mormodes (Orchidaceae), Scheelea (Palmae), Alibertia, Amaouia and Randia (2 spp.) (Rubiaceae).

Fewer pistillate flowers were studied as they are less frequent. A total of 76 dioecious species with pistillate flowers were studied. The average flower length for these was 6.76 mm. However, again, if all flowers more than 1 cm long are excluded, the average length is only 3.1 mm. For the 19 species with normal maximum flower length of 1 cm or more, the average is 17.7 mm. In addition to the genera listed for staminate flowers with flowers more than 1 cm long, the following species have pistillate flowers more than 1 cm long: Acalypha macrostachya, Alchornea latifolia (only if styles are included) (Euphorbiaceae), Gynerium sagittatum (Graminae) and Triplaris cumingiana (Polygonaceae).

Though this study did show sexual dimorphism in flower size, it is not believed to be as important on BCI as was shown by Bawa and Opler (1975) in Guanacaste (Table 3). Only 29 species (27%) showed any noticeable sexual dimorphism in flower size, though pistillate flowers of an additional 6 species were not studied owing to inavailability of flowers. Thirteen species showed pistillate

flowers to be smaller than their staminate counterpart rather than larger (16 species). However, the mean percentage difference in flower size was 60% for the group with pistillate flowers larger than staminate, and only 26% for the group with pistillate flowers smaller than staminate (see Table 3). In comparison Bawa and Opler (1975) found 14 of 20 species (70%) measured, with staminate flowers smaller than pistillate.

Perhaps more important than perianth size is the size and coloration of the sexual parts. For example, on many species the perianth is inconspicuous in comparison to the cluster of numerous stamens. Thus, in Xylosma (Flacourtiaceae) the staminate flower with its large cluster of stamens is showier than the pistillate flower with its inconspicuous stigma. On the other hand, the showy, much-divided style of such species as Acalypha macrostachya (Euphorbiaceae) make the pistillate flowers more conspicuous than the staminate flowers.

Also important yet difficult to compare is the shape, disposition and density of the inflorescence, which may replace the individual flowers as the pollinating unit, such as in the Moraceae. In that family individual flowers are inconspicuous and perhaps individually unimportant but the shape, size and coloration of the inflorescence are no doubt significant in attracting pollinators. While it is certainly true that most dioecious species have small flowers, relatively few dioecious species also have solitary flowers or otherwise have their flowers arranged in inconspicuous clusters. Thus insects are probably not attracted to individually inconspicuous dioecious flowers but rather to clusters of flowers which form attractive pollination units. Many dioecious species in the BCI flora have flowers which are so aggregated that the functional attraction unit must be the flower aggregate or inflorescence rather than individual flowers. These include Iresine celosia, Struthanthus orbicularis, Chamaedorea wendlandii, and Scheelea zonensis, as well as a large percentage of the Moraceae including Cecropia spp., Coussapoa Spp., Maquira costaricana, Perebea xanthochyma, Pourouma aspera and Pseudolmedia spuria. Also included here is one gymnosperm, Gnetum leyboldii

var. woodsoniana, whose microsporangia are densely aggregated.

2. The inconspicuous nature of flowers of dioecious species is partly due to their usually pale color. Bawa and Opler (1975) have indicated that most have colors ranging from white to yellow or pale green. Added to this on the basis of my studies would be brownish flowers, Viola (Myristicaceae) (2 species), the brownish-purple flowers of Coccoloba acapulcensis (Polygonaceae), the violet-purple flowers of Dioscorea haenkeana and D. macrostachya (Dioscoreaceae), and the reddish flowers of Neea amplifolia (Nyctaginaceae), Coccoloba acuminata, (Polygonaceae) and Trattinnickia aspera (Burseraceae). The remainder of the dioecious species on BCI are the colors mentioned by Bawa and Opler (see Table 4).

3. In comparing dioecious and hermaphroditic species or genera, no general statement about flower size can be made. Some families, such as Anacardiaceae, Amaranthaceae, Compositae, Boraginaceae, Flacourtiaceae, Sapindaceae, Sapotaceae, Simaroubaceae and Lauraceae, have dioecious species with flowers averaging smaller than their hermaphroditic sibling genera but the degree of difference is not always significant. Some families have dioecious species with flowers averaging as large as or larger than their cogeners. Bawa and Opler have already noted this in the Rubiaceae. Other families which show this include the Guttiferae, Loranthaceae and Myrsinaceae. Still other families had no hermaphroditic species in Panama with which they could be compared and thus were not considered. These include such families as Burseraceae, Smilacaceae, Caricaceae, Euphorbiaceae, Meliaceae, Monimiaceae, Dioscoreaceae, Hydrocharitaceae, Gnetaceae, Myristicaceae, Nyctaginaceae, Rafflesiaceae, Palmae, Rutaceae, Urticaceae, Moraceae and Menispermaceae.

The only dioecious representative of the Gramineae on BCI has staminate flowers which are smaller (less than 3 mm) than the flowers of the average hermaphroditic grass species, but has pistillate flowers which are up to 12 mm long,

longer than the flowers of the average hermaphroditic grass species. Dioecious representatives of the Polygonaceae also show an inconsistent pattern. Coccoloba coronata has flowers smaller than the average hermaphroditic polygonaceous species. Triplaris cumingiana has staminate flowers smaller than average but pistillate flowers larger than the average hermaphroditic polygonaceous flower.

SUMMARY

The breeding systems of the Barro Colorado Island flora in the isthmus of Panama were analyzed. Of the 1,212 native species in the flora, 286 (24%) have unisexual flowers. Of these, 106 (9%) are dioecious, 132 (11%) are monoecious (4 are monoecious or dioecious and are included in both categories), and 52 (4%) are polygamous. Fifteen percent of the medium to large sized trees are monoecious, while 21% are dioecious. Eleven percent of the herbs are monoecious, and only 2% are dioecious. Small trees and shrubs are 7% monoecious and 12% dioecious. These figures compare favorably with studies by Bawa and Opler (1975) in the Comelco region of Guanacaste in Costa Rica. However, they reported no scandent dioecious species, whereas by contrast, 20% of the dioecious species in the BCI flora are scandent (8% of all scandent species).

The average size of staminate and pistillate flowers for all species is 7.6 mm and 6.8 mm respectively. If all flowers more than 1 cm long are excluded from consideration, the average size for staminate and pistillate flowers is 3.16 mm and 3.12 mm respectively. Only 29 species (27%) of all dioecious species show any noticeable sexual dimorphism in flower size. Thirteen of these had staminate flowers larger than pistillate. Bawa and Opler reported 14 of 20 species measured in Costa Rica with pistillate flowers larger than staminate ones. The differences in staminate and pistillate flower size for dioecious species are thus less significant than the differences in the flora of the Comelco region of Costa Rica reported by Bawa and Opler.

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TABLE 1

Habit Type	Total Native Species	Herma- phroditic	Monoecious	Dioecious	Polygamous
Medium to Large Trees (more than 10 m)	211	133	32** 15%	45** 21%	3 1%
Small Trees and/or Shrubs (including hemiepiphytic and parasitic shrubs)	270	212	19* 7%	32* 12%	9 3%
Scandent Plants	265	189	31 12%	21 8%	23 9%
Herbs (including aquatic, epiphytic and parasitic herbs and palmettoes)	466	392	50* 11%	8* 2%	17 4%
TOTAL NATIVE PHANEROGAMS	1,212	926	132 11%	106 9%	52 4%
TOTAL SPECIES WITH UNISEXUAL FLOWERS 286 (24%)					

** Two species considered both monoecious and dioecious

* One species considered both monoecious and dioecious

TABLE 2 Flower length of dioecious species on Barro Colorado Island

Total dioecious species on BCI = 106	No. of Flowers studies n	All dioecious species		Largest Flowers less than 1 cm			Largest Flowers 1 cm or more		
		Aver. Lgth.	Stand. Error	n	Aver. Lgth.	Stand. Error	n	Aver. Lgth.	Stand. Error
Staminate	97	7.61mm	20.12	81	3.16mm	1.75	16	30.1mm	42.58
Pistillate	76	6.76mm	8.41	57	3.12mm	1.62	19	17.7mm	10.78

TABLE 3 Sexual Dimorphism on BCI

	Number of Species	Average Normal Maximum size of staminate flowers	Average Normal Maximum size of pistillate flowers	Difference $\sigma - \text{♀}$		Percentage Difference $\frac{\sigma - \text{♀}}{\text{♀}}$	
				Aver.	Stand. error	Aver.	Stand. error
Staminate fls. larger than pistillate	13	3.8 mm	2.7 mm	1.45 mm	1.5 mm	26%	11.8%
Pistillate fls. larger than staminate	16	2.5 mm	8.0 mm	5.51 mm	4.7 mm	60%	21.5%

TABLE 4 Flower Color of Dioecious Species

Color	No. of Species
Yellow	2
Yellow-green or Greenish-yellow	7
Green	33**
Pale Green or Greenish-white	20
White	36*
Subtotal	98
Brown	2
Reddish, Purplish or marked with reddish	6***
TOTAL	106
* Includes <i>Catopsis sessiliflora</i>	Greenish-yellow and white
<i>Cecropia insignis</i>	Whitish-green and whitish-yellow
<i>Clusia odorata</i>	White to pink
** Includes <i>Mormodes powellii</i>	Green, yellow-brown or cream
*** Includes <i>Trattinnickia aspera</i>	Dull red tinged with green
<i>Dioscorea macrophylla</i>	Violet-purple with green edges
<i>Coccoloba acapulcensis</i>	Brownish-purple

TABLE 5 Monoecious species in the BCI Flora

Family	Species	Habit*
Alismataceae	<i>Sagittaria lancifolia</i> L.	H
Amaranthaceae	<i>Amaranthus viridis</i> L.	H
Araceae	<i>Dieffenbachia longispatha</i> Engler & Krause	H
	<i>D. oerstedii</i> Schott	H
	<i>D. pittieri</i> Engler & Krause	H
	<i>Homalomena wendlandii</i> Schott	H
	<i>Montrichardia arborescens</i> (L.) Schott	H
	<i>Philodendron fragrantissimum</i> (Hook.) Kunth	H
	<i>P. grandipes</i> Krause	H
	<i>P. guttiferum</i> Kunth	V
	<i>P. hederaceum</i> (Jacq.) Schott	V
	<i>P. inaequilaterum</i> Liebm.	V
	<i>P. inconcinnum</i> Schott	V
	<i>P. nervosum</i> (Schultes & Schultes) Kunth	H
	<i>P. panamense</i> Krause	H
	<i>P. pterotum</i> C. Koch & Aug.	H
	<i>P. radiatum</i> Schott	H
	<i>P. sagittifolium</i> Liebm.	H
	<i>P. scandens</i> C. Koch & Sellow	V
	<i>P. tripartitum</i> (Jacq.) Schott	V
	<i>Pistia stratiotes</i> L.	H
	<i>Syngonium erythrophyllum</i> Birdsey ex Bunting	V
	<i>S. podophyllum</i> Schott	V
	<i>Xanthosoma helleborifolium</i> (Jacq.) Schott	H
	<i>X. nigrum</i> (Vell.) Stellfeld	H
	<i>X. pilosum</i> C. Koch & Aug.	H
Begoniaceae	<i>Begonia filipes</i> Benth.	H
	<i>B. guaduensis</i> H.B.K.	H
	<i>B. patula</i> Haw.	H
Bromeliaceae	** <i>Catopsis sessiliflora</i> (R. & P.) Mez	H

TABLE 5 continued

Ceratophyllaceae	Ceratophyllum demersum L.	H
Compositae	Clibadium surinamense L.	S
Cucurbitaceae	Cayaponia glandulosa (P. & E.) Cogn.	L
	C. granatensis Cogn.	V
	C. racemosa (Sw.) Cogn.	V
	Fevillea cordifolia L.	V
	***Gurania coccinea Cogn.	V
	G. makoyana (Lem.) Cogn.	V
	G. megistantha Donn. Sm.	V
	Melothria pendula L.	V
	M. trilobata Cogn.	V
	Momordica charantia L.	V
	Posadaea sphaerocarpa Cogn.	V
	***Psiguria bignoniacea (P. & E.) Wunderlin	V
	P. warscewiczii (Hook.f.) Wunderlin	V
	Sicydium coriaceum Cogn.	V
Cyclanthaceae	Asplundia alata Harling	H
	Carludovica drudei Mast.	H
	C. palmata Ruiz & Pavon	H
	Cyclanthus bipartitus Poit.	H
	Ludovia integrifolia (Woods.) Harling	V
Cyperaceae	Calyptracarya glomerulata (Brongn.) Urban	H
	Scleria eggersiana Boeckl.	H
	S. macrophylla Presl	H
	S. mitis Bergius	H
	S. pterota Presl	H
	S. secans (L.) Urban	V
Euphorbiaceae	Acalypha arvensis Poepp.	H
	A. diversifolia Jacq.	S
	**A. macrostachya Jacq.	ST
	Chamaesyce hirta (L.) Millsp.	H
	C. hypericifolia (L.) Millsp.	H
	C. hyssopifolia (L.) Small	H
	C. thymifolia (L.) Millsp.	H
	Croton billbergianus Muell.-Arg.	ST
	C. hirtus L'Her.	H
	C. panamensis (Klotzsch) Muell.-Arg.	T

*** Gurania and Psiguria are usually functionally dioecious with long lapses between staminate and pistillate sexual states.

TABLE 5. continued

Euphorbiaceae	<i>Dalechampia cissifolia</i>		
	Poepp. subsp. <i>panamensis</i> (Pax & Hoffm.) Webster	V	
	<i>D. dioscoreifolia</i> Poepp.	V	
	<i>D. tiliifolia</i> Lam.	V	
	<i>Garcia nutans</i> Vahl	T	
	<i>Hura crepitans</i> L.	T	
	<i>Mabea occidentalis</i> Benth.	ST	
	<i>Omphalea diandra</i> L.	L	
	<i>Phyllanthus acuminatus</i> Vahl	S	
	<i>P. amarus</i> Schum.	H	
	<i>P. urinaria</i> L.	H	
	<i>Poinsettia heterophylla</i> (L.) Klotzsch & Gke.	H	
	<i>Sapium aucuparium</i> Jacq.	T	
	<i>S. caudatum</i> Pittier	T	
	Graminae	<i>Lithachne pauciflora</i> (Sw.) Beauv. ex Poir.	H
		<i>Olyra latifolia</i> L.	H
		<i>Pharus latifolius</i> L.	H
<i>P. parvifolius</i> Nash		H	
Loranthaceae	<i>Phorandendron piperoides</i> (H.B.K.) Trel.	S	
	<i>P. quadrangule</i> (H.B.K.) Krug & Urb.	S	
Meliaceae	<i>Cedrela odorata</i> L.	T	
Monimiaceae	<i>Siparuna guianensis</i> Aubl.	S	
Moraceae	<i>Brosimum alicastrum</i> (Pitt.) C.C. Berg ssp. <i>bolivarense</i> (Pitt.) C.C. Berg	T	
	** <i>Castilla elastica</i> Sessé	T	
	<i>Ficus bullenei</i> I.M. Johnston	T	
	<i>F. citrifolia</i> P. Mill.	T	
	<i>F. colubrinae</i> Standley	T	
	<i>F. costaricana</i> (Liebm.) Miq.	T	
	<i>F. dugandii</i> Standley	T	
	<i>F. insipida</i> Willd.	T	
	<i>F. maxima</i> P. Mill.	T	
	<i>F. nymphiifolia</i> P. Mill.	T	
	<i>F. obtusifolia</i> H.B.K.	T	
	<i>F. paraensis</i> (Miq.) Miq.	T	
	<i>F. perforata</i> L.	T	
	<i>F. pertusa</i> L.f.	T	
	<i>F. popenoei</i> Standley	T	
	<i>F. tonduzii</i> Standley	T	

TABLE 5 continued

Moraceae	<i>F. trigonata</i> L.	T
	<i>F. yoponensis</i> Desv.	T
	<i>Poulsenia armata</i> (Miq.) Standley	T
Orchidaceae	<i>Catesetum bicolor</i> Klotzsch	H
	<i>C. viridiflavum</i> Hook.	H
Palmae	<i>Astrocaryum standleyanum</i> Bailey	T
	<i>Bactris barronis</i> Bailey	ST
	<i>B. coloniata</i> Bailey	ST
	<i>B. coloradonis</i> Bailey	ST
	<i>B. major</i> Jacq.	ST
	<i>Desmoncus isthmus</i> Bailey	V
	<i>Elaeis oleifera</i> (H.B.K.) Cortes	ST
	<i>Geonoma cuneata</i> Wendl. ex Spruce	S
	<i>G. interrupta</i> (R. & P.) Mart.	S
	<i>G. procumbens</i> Wendl. ex Spruce	S
	<i>Oenocarpus panamanus</i> Bailey	T
	** <i>Scheelea zonensis</i> Bailey	T
	<i>Socratea durissima</i> (Oerst.) Wendl.	T
	<i>Synechanthus warscewiczianus</i> Wendl.	ST
	Sterculiaceae	<i>Sterculia apetala</i> (Jacq.) Karst.
<i>Trichospermum mexicanum</i> (L.) Baill.		T
Tiliaceae	<i>Typha domingensis</i> Persoon	H
Typhaceae	<i>Celtis iguanaeus</i> (Jacq.) Sarg.	L
Ulmaceae	<i>Trema micrantha</i> (L.) Blume	T
Urticaceae	<i>Boehmeria cylindrica</i> (L.) Sw.	H
	<i>Myriocarpa yzabalensis</i> (Donn. Sm.) Killip	ST
	<i>Pilea microphylla</i> (L.) Liebm.	H
	<i>Pouzolzia obliqua</i> (Poepp.) Wedd.	L

* H=Herb; V=Vine; L=Liana; S=Shrub; ST=Small Tree
T=Tree

** May be either monoecious or dioecious.

TABLE 6 Polygamous species in the BCI Flora

Family	Species	Habit*
Araliaceae	Oreopanax capitatus (Jacq.) Dec. & Planch	T
Celastraceae	Maytenus schippii Lundell	ST
Compositae	Baltimora recta L.	H
	Chaptalia nutans (L.) Polak.	H
	Conyza apurensis Kunth	H
	C. bonariensis (L.) Cronq.	H
	Eclipta alba (L.) Hassk.	H
	Erechtites hieracifolia (L.) Raf. var. cacalioides (Fischer ex Spreng.) Griseb.	H
	Melampodium divaricatum (L.C. Rich.) DC.	H
	Pluchea odorata (L.) Cass.	H
	Schistocarpha oppositifolia (O. Ktze.) Rydb.	H
	Synedrella nodiflora (L.) Gaertn.	H
	Tridax procumbens L.	H
	Verbesina gigantea Jacq.	H
	Wedelia trilobata (L.) Hitchc.	H
Cyperaceae	Cladium jamaicense Crantz	H
	Rhynchospora cephalotes (L.) Vahl	H
	R. corymbosa (L.) Britt.	H
	R. micrantha Vahl	H
Dilleniaceae	Tetracera hydrophila Tr.&Pl.	L
	T. portobellensis Beurl.	L
	T. volubilis L.	L
Guttiferae	**Tovomitopsis nicaraguensis (Oerst.) Tr.&Pl.	ST
	Vismia billbergiana Beurl.	ST
Sapindaceae	Allophylus psilospermus Radlk.	ST
	Cupania cinerea Poepp. & Endl.	ST
	C. latifolia Kunth	T
	C. rufescens Tr. & Pl.	T
	C. sylvatica Seem.	ST

* H=Herb; V=Vine; L=Liana; S=Shrub; ST=Small Tree
T=Tree

**Based on flower morphology only; fruit set not observed.

TABLE 6. continued

Sapindaceae	<i>Paullinia baileyi</i> Standley	L
	<i>P. bracteosa</i> Radlk.	L
	<i>P. fibrigera</i> Radlk.	L
	<i>P. fuscescens</i> H.B.K. var. <i>glabrata</i> Croat	L
	<i>P. glomerulosa</i> Radlk.	L
	<i>P. pinnata</i> L.	L
	<i>P. pterocarpa</i> Tr. & Pl.	L
	<i>P. rugosa</i> Benth. ex Radlk.	L
	<i>P. turbacensis</i> H.B.K.	L
	<i>Serjania atrolineata</i> Suav. & Wright	L
	<i>S. circumvallata</i> Radlk.	L
	<i>S. cornigera</i> Turcz.	L
	<i>S. decapleuria</i> Croat	L
	<i>S. paucidentata</i> DC.	L
	<i>S. mexicana</i> (L.) Willd.	L
	<i>S. pluvialiflorens</i> Croat	L
	<i>S. rhombea</i> Radlk.	L
	<i>S. trachygona</i> Radlk.	L
	<i>Talisia nervosa</i> Radlk.	ST
	<i>T. princeps</i> Oliver	ST
<i>Thinouia myriantha</i> Tr. & Pl.	L	
Tiliaceae	*** <i>Heliocarpus popayanensis</i> H.B.K.	ST
Vitaceae	<i>Vitis tiliifolia</i> H. & B. ex R. & S.	L

***Based on flower morphology on only 2 individuals.

TABLE 7 Dioecious species in the BCI Flora

Family	Species	Habit*
Amaranthaceae	<i>Iresine celosia</i> L.	H
Anacardiaceae	<i>Astronium graveolens</i> Jacq.	T
Boraginaceae	<i>Cordia panamensis</i> Riley	ST
Bromeliaceae	** <i>Catopsis sessiliflora</i> (R.& P.) Mez.	H
Burseraceae	*** <i>Bursera simaruba</i> (L.) Sarg.	T
	<i>Protium costaricense</i> (Rose) Engler	T
	<i>P. panamense</i> (Rose) I.M. Johnston	T
	<i>P. tenuifolium</i> var. <i>sessiliflorum</i> (Rose) Porter	T
	<i>Tetragastris panamensis</i> (Engler) O. Kuntze	T
	<i>Trattinnickia aspera</i> (Standley) Swart	T
Caricaceae	<i>Carica cauliflora</i> Jacq.	ST
	<i>Jacaratia spinosa</i> (Aubl.) A. DC.	T
Compositae	<i>Baccharis trinervis</i> Persoon	S
Dioscoreaceae	<i>Dioscorea haenkeana</i> Presl	V
	<i>D. macrostachya</i> Benth.	V
	<i>D. polygonoides</i> H. & B. ex Willd.	V
	<i>D. sapindoides</i> Presl	V
	<i>D. urophylla</i> Hemsl.	V
Ebenaceae	<i>Diospyros arthanthifolia</i> Mart.	T
Euphorbiaceae	** <i>Acalypha macrostachya</i> (Jacq.) Hemsl.	ST
	<i>Adelia triloba</i> (Muell.-Arg.) Hemsl.	S
	<i>Alchornea costaricensis</i> Pax & Hoffm.	T
	<i>A. latifolia</i> Sw.	T
	<i>Drypetes standleyi</i> Webster	T
	<i>Hyeronima laxiflora</i> (Tul.) Muell.-Arg.	T
	<i>Margaritaria nobilis</i> L.f.	ST
Flacourtiaceae	<i>Xylosma chloranthum</i> Donn.Sm.	ST
	<i>X. oligandrum</i> Donn.Sm.	ST
Gnetaceae	<i>Gnetum leyboldii</i> Tul. var. <i>woodsonianum</i> Markgr.	L
Graminae	<i>Gynerium sagittatum</i> (Aubl.) Beauv.	H
Guttiferae	<i>Clusia odorata</i> Seem.	ST

TABLE 7 continued

Guttiferae	Havetiopsis flexilis Pl.&Tr.	ST
	***Rheedia acuminata Pl.&Tr.	ST
	***R. edulis Tr. & Pl.	ST
	Tovomita longifolia (L.C.Rich.) Hochr.	ST
	T. stylosa Hemsf.	ST
Hydrocharitaceae	Hydrilla verticillata (L.f.) Royle	H
	Limnobium stoloniferum (F. Meyer) Griseb.	H
Lauraceae	Ocotea cernua (Nees) Mez	T
	O. oblonga (Meisn.) Mez	T
	O. pyramidata Blake ex T. S. Brandegee	T
	O. skutchii C. K. Allen	T
Loranthaceae	Struthanthus orbicularis (H.B.K.) Blume	S
Malvaceae	Hampea appendiculata (J.D.Sm.) Standley var. longicalyx Fryxell	T
	Meliaceae	Guarea glabra Vahl
G. multiflora Juss.		T
Trichilia cipo (A.Juss.) C. DC.		T
T. hirta L.		ST
T. montana H.B.K.		ST
Menispermaceae	T. verrucosa C. DC.	T
	Abuta panamensis (Standley) Krukoff & Barneby	L
	A. racemosa (Thunb.) Tr.&Pl.	L
	Chondrodendron tomentosum R. & P.	L
	Cissampelos pareira L.	V
	C. tropaeolifolia DC.	V
	Odontocarya tamoides (DC.) Miers var. canescens (Miers) Barneby	V
	O. truncata Standley	V
	Siparuna pauciflora (Beurl.) A. DC.	ST
Moraceae	**Castilla elastica Sesse	T
	Cecropia insignis Liebm.	T
	C. longipes Pittier	T
	C. obtusifolia Bertol.	ST
	C. peltata L.	T

TABLE 7 continued

Moraceae	<i>Coussapoa magnifolia</i> Trec.	ST
	<i>C. panamensis</i> Pitt.	T
	<i>Dorstenia contrajerva</i> L.	H
	<i>Maquira costaricana</i> (Standley) C.C.Berg	T
	<i>Olmedia aspera</i> R. & P.	ST
	<i>Perebea xanthochyma</i> Karst.	ST
	<i>Pourouma guianensis</i> Aubl.	T
	<i>Pseudolmedia spuria</i> (Sw.) Griseb.	T
	<i>Sorocea affinis</i> Hemsl.	ST
	<i>Trophis racemosa</i> (L.) Urban	T
Myristicaceae	<i>Virola sebifera</i> Aubl.	T
	<i>V. surinamensis</i> (Rol.) Warb.	T
Myrsinaceae	<i>Stylogyne standleyi</i> Lundell	ST
Nyctaginaceae	<i>Guapira standleyanum</i> Woodson	T
	<i>Neea amplifolia</i> Donn. Sm.	S
	<i>Pisonia aculeata</i> L.	L
Orchidaceae	<i>Mormodes powellii</i> Schlechter	H
Palmae	<i>Chamaedorea wendlandiana</i> (Oerst.) Hemsl.	S
	** <i>Scheelea zonensis</i> Bailey	T
Polygonaceae	<i>Coccoloba acapulcensis</i> Standley	ST
	<i>C. acuminata</i> H.B.K.	ST
	<i>C. coronata</i> Jacq.	T
	<i>C. manzanillensis</i> Beurl.	T
	<i>C. parimensis</i> Benth.	L
	<i>Triplaris cumingiana</i> Fischer & Meyer	T
	<i>Apodanthes caseariae</i> Poit.	H
Rafflesiaceae	<i>Alibertia edulis</i> A. Rich.	ST
	<i>Amaioua corymbosa</i> H.B.K.	T
Rubiaceae	<i>Randia armata</i> (Sw.) DC.	ST
	<i>R. formosa</i> (Jacq.) K. Schum.	ST
	<i>Zanthoxylum belizense</i> Lundell	T
Rutaceae	<i>Z. panamense</i> P. Wilson	T
	<i>Z. procerum</i> Donn. Sm.	T
	<i>Z. setulosum</i> P. Wilson	T
	**** <i>Pouteria stipitata</i> Cronq.	T
Sapotaceae	<i>Picramnia latifolia</i> Tul.	ST
	<i>Simarouba amara</i> Aubl.	T
Simaroubaceae	<i>Smilax lanceolata</i> L.	V
	<i>S. mollis</i> H. & B. ex Willd.	V
	<i>S. panamensis</i> Morong.	V
	<i>S. spinosa</i> Mill.	V

TABLE 7 continued

Smilacaceae	<i>S. spissa</i> Killip & Morton	V
Urticaceae	<i>Urera eggersii</i> Hieron.	V

* H=Herb; V=Vine; L=Liana; S=Shrub; ST=Small Tree
T=Tree

** May be either monoecious or dioecious

*** Polygamodioecious

**** This species is doubtfully dioecious. The 3 other *Pouteria* species on BCI are thus also suspect.

Figure 1a. Distribution of species based on maximum normal length of staminate flowers

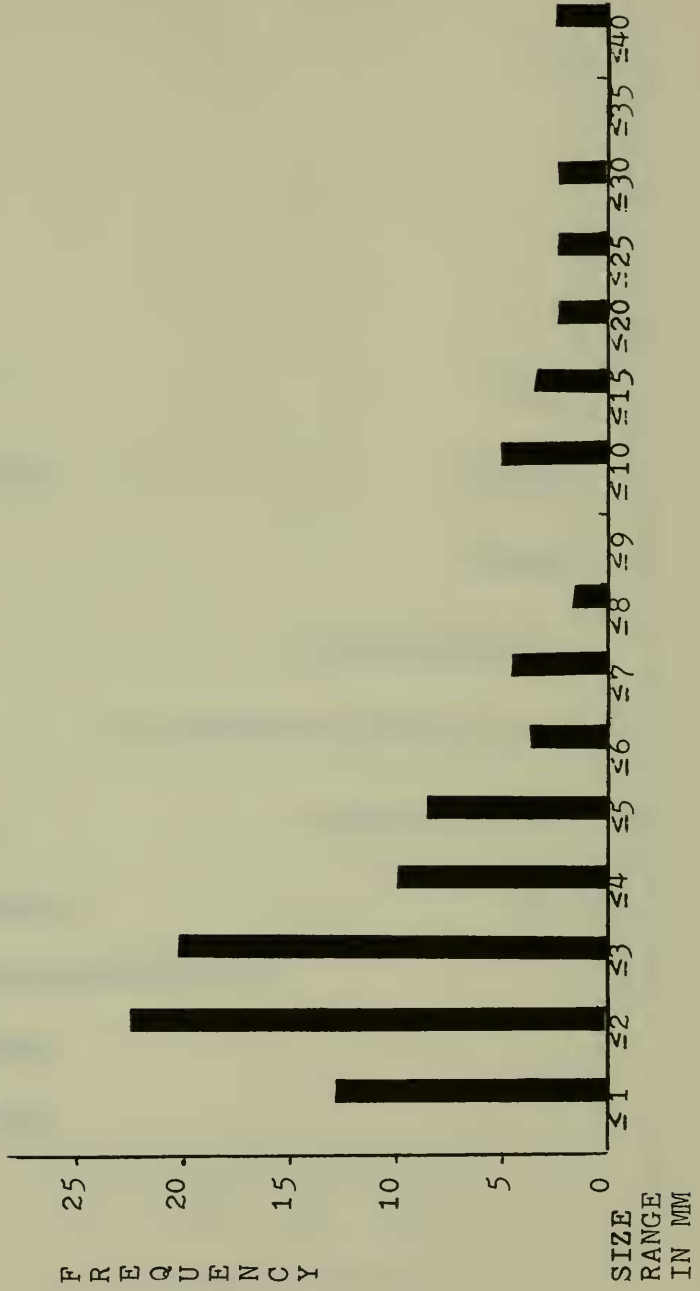


Figure 1b. Distribution of species based on maximum normal length of pistillate flowers.

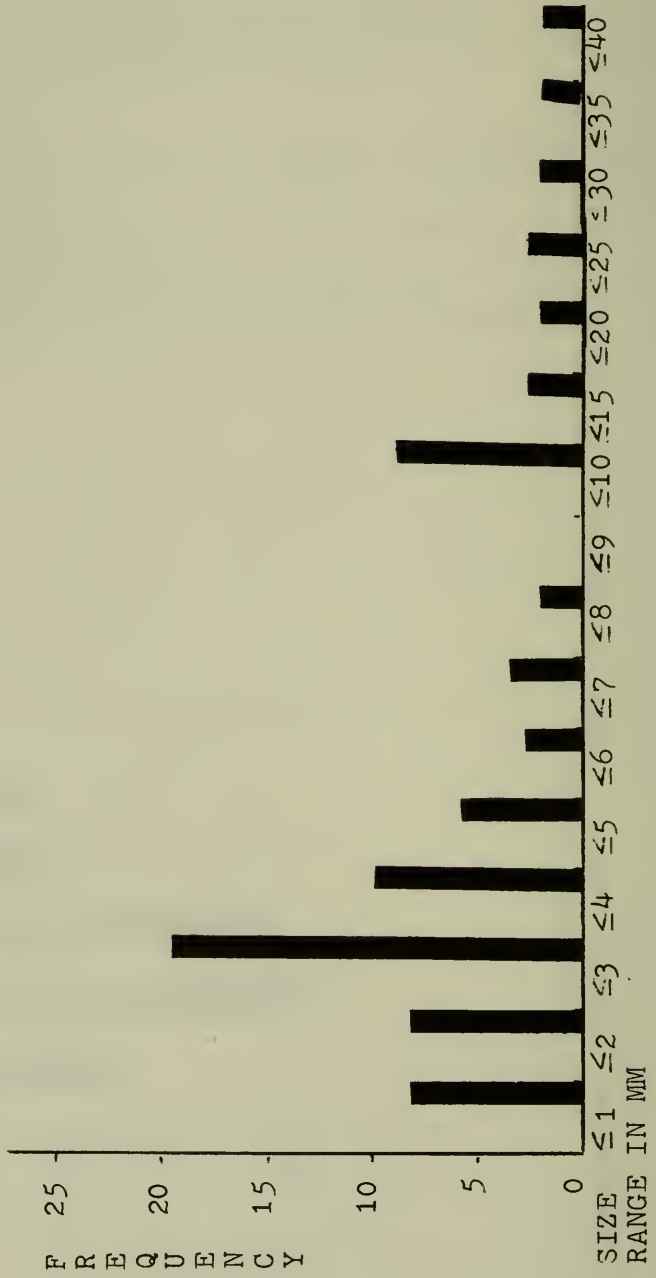


Figure 2a. Distribution of normal maximum staminate flower lengths.

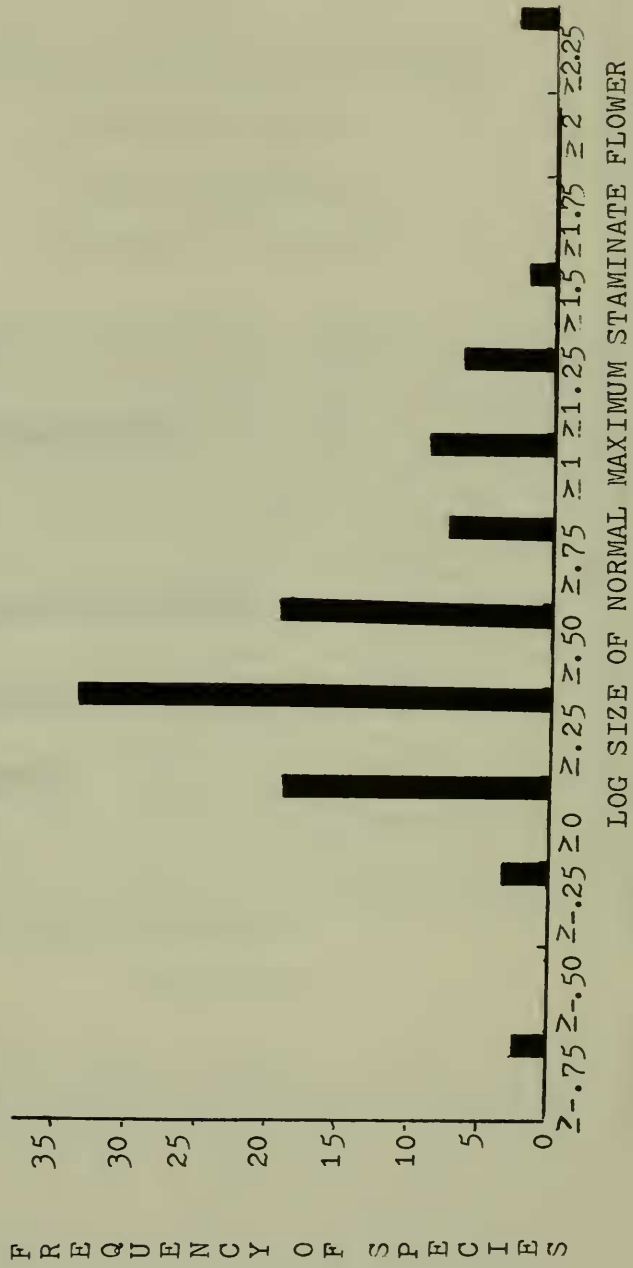


Figure 2b. Distribution of normal maximum pistillate flower lengths

