Selbyana 9: 149–155

CHARACTERISTICS AND PHYTOGEOGRAPHICAL ANALYSIS OF A SUBSET OF THE FLORA OF LA SELVA (COSTA RICA)

BARRY E. HAMMEL*

Department of Botany, Duke University,
Durham, North Carolina 27706

ABSTRACT. Approximately 75 percent of the species of Cecropiaceae, Clusiaceae, Cyclanthaceae, Lauraceae, Marantaceae, and Moraceae are rare or uncommon at La Selva, 30 percent are dioecious, most are probably insect pollinated and bird dispersed, 30 percent are epiphytic, and 42 percent are found only in primary forest. To a certain degree, these characteristics are predictive of the entire flora and to the flora of the Caribbean lowland region in general. La Selva shares more species and genera in this subset of its flora with Barro Colorado Island, Panama, than with Río Palenque Science Center, Ecuador. In general, the principal phytogeographic affinities of La Selva, as demonstrated by these six families, are to the south.

Six of the family treatments for the Flora of La Selva (Hammel, 1984) constitute the subset of the La Selva flora on which the present analysis is based. Floras of two other lowland sites in the neotropics have recently been completed (Croat, 1978; Dodson & Gentry, 1978), affording the opportunity to make floristic comparisons between La Selva and these geographically distant but climatically similar areas. The analysis of the characteristics and affinities of a subset of the La Selva flora is intended as an estimate of these same features for the whole flora. It may also be predictive of the larger Caribbean-lowland floristic region.

These particular families were chosen because they were poorly known and poorly collected throughout their range. Genera such as *Asplundia* (Cyclanthaceae), *Calathea* (Marantaceae), *Clusia* (Clusiaceae), *Ocotea* (Lauraceae), and *Ficus* (Moraceae) reach their highest diversity in areas of the wet tropics like La Selva. They also need special attention to collect adequately and to identify because in many cases they make bulky specimens and preserve poorly.

MATERIALS AND METHODS

Field Studies

La Selva Biological Station covers an area of approximately 1,400 ha (5.44 square miles) in the Caribbean lowlands of northeastern Costa Rica. It lies at a transition between Tropical Premontane Wet Forest and Tropical Wet Forest Life Zones (Hartshorn, 1983). The average annual rainfall is very nearly 4,000 mm. Although the area is usually described as continuously wet or having no effective dry season (cf. Hartshorn, 1983), the rainfall record for a 26 year period (Organization for Tropical Studies, unpubl.) shows a distinctly drier season from January through April; only one-fifth of the annual rain falls within the first one-third of the year.

The identifications, descriptions, and observations (Hammel, 1984), which form the basis of the present analysis, derive from a total of two years of fieldwork at La Selva, including ten months beginning February 1980, several three to five month periods between 1981 and 1982 and a two week visit in August of 1983. Plants were collected from nearly every part of the property. However, the Western Annex was not included in the study until after the first year of collecting; the original property has been much more intensively collected. During the course of the fieldwork, collecting walks were made across the width of the original property at about every 200 m interval.

Field notes were written from fresh material and for most species of Lauraceae and *Clusia* flowers were preserved in 70 percent ethanol. Information on flowering and fruiting phenology was summarized from herbarium specimens as well as from on-site observations. Distributional ranges were taken from the recent literature in conjunction with examination of herbarium specimens. Almost all of the information concerning distribution and abundance within La Selva came from personal observation.

Herbarium Studies

Identifications were based on examination of approximately 600 collections of the families from La Selva, as well as other herbarium material from both Central and South America. Representative specimens for a few abundantly collected species and all specimens examined of the remaining species are cited in the original thesis.

* Present address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299.

The Comparative Field Sites

Barro Colorado Island (BCI) lies in the center of a man-made lake mid-way between the Atlantic and Pacific coasts in central Panama. It has a Life Zone classification of Tropical Moist Forest, an effective four month dry season, and an average annual rainfall of 2,750 mm (Croat, 1978). The island is slightly larger than La Selva but its reported total of 1,316 species (plus 15–20 additions since publication; Gentry, pers. comm.) is probably lower than the total at La Selva (Hammel & Grayum, 1982). The Río Palenque Science Center (RPSC) of central coastal Ecuador is tentatively classified as Tropical Premontane Wet Forest with an estimated annual rainfall between 2,650 and 3,000 mm (Dodson & Gentry, 1978). It has a five month dry season with relatively cool but rainy nights (Dodson & Gentry, 1978). Río Palenque is roughly one-ninth the size of La Selva but has more than half as many species (1,032 species, plus over 50 since publication, Gentry, pers. comm.) as the estimated total for La Selva (2,000 species).

Results and Discussion

Composition of the Flora Subset

Characteristics of the entire La Selva flora and perhaps of the flora of the Caribbean lowlands in general, can be inferred from detailed examination of a subset of the flora (Table 1). This will be useful for comparative studies during the interim before the completion of the flora project and in view of the likelihood that the region of the Caribbean lowlands, being so much larger and unprotected, may never be thoroughly known.

Abundance. Approximately 75 percent of the species are known from a few individuals or from a few small populations at La Selva. Some of these (e.g., *Calathea donnell-smithii, C. foliosa*) appear to be rare throughout their range, whereas others such as *Tovomita weddelliana* are more common elsewhere. Some species that are rare at La Selva, such as *Persea rigens,* are relatively common in areas very close to La Selva (pers. obs.).

Sexuality. The portion of dioecious species (30 percent) in this subset of the flora (Table 1) is high relative to other similar forests. Bawa (1980) reported 66 (22 percent) dioecious species among the 388 trees and shrubs he considered at La Selva. Only about 9 percent of all the species on BCI are dioecious (Croat, 1978). In terms of sexuality, these families are not a random subset and probably are not representative of the larger flora.

Pollination. Being primarily insect pollinated (pers. obs.), the species in this subset are typical of wet tropical lowland forests (Bawa et al., 1985). One species, *Symphonia globulifera,* is hummingbird pollinated (Beach, pers. comm.). Two species, *Trophis involucrata* (Bawa & Crisp, 1980) and *T. racemosa* (pers. obs.), are wind pollinated.

Dispersal. As with pollination, fruit (seed) dispersal in this subset of the flora is primarily by animal vectors. *Marila laxiflora* is the only species with wind-dispersed seeds. The fruits of the remaining species provide some reward to possible animal dispersers. The majority of species appear to be bird-dispersed, but some taxa are probably mammal-dispersed as well (e.g., *Asplundia* spp., *Calophyllum brasiliense, Ficus* spp., *Rheedia edulis, Symphonia globulifera, Vismia* spp.). To the extent that fleshy fruits are associated with dioecy (Bawa, 1980; Givnish, 1980), the high percentage of animal-dispersed species in this subset is again not representative of the whole flora. Nevertheless, the high percentage is consistent with the demonstrated increase in percentage of animal-dispersed species from dry to wet forest habitats (Gentry, 1982a).

Habit and habitat. The percentage of epiphytes in the flora subset (Table 1) is about the same (30 percent) as an estimate, including vines and lianas, for the entire flora (Hammel, unpubl.) and is also similar to estimates for the wet lowland neotropics in general (Gentry, pers. comm.). Over half of the species in this study occur in primary upland forest (Table 1). The next most species-rich habitat for these taxa is the forest along the Puerto Viejo and Sarapiquí rivers. Together, these two relatively undisturbed habitats account for nearly 90 percent of the species in the subset.

Comparison with Barro Colorado Island and Río Palenque

The six families under study comprise a total of 123 species in 42 genera at La Selva; on BCI 75 species in 36 genera are represented; and at RPSC 78 species in 31 genera (excluding cultivated species) are found. La Selva shares 71 percent and 30 percent of its genera and species (respectively) with BCI, 59 percent and 23 percent, respectively, with RPSC, and 51 percent and 15 percent, respectively, with both areas (Table 2).

Ficus is the most species-rich genus within the subset at each of the sites; the number of species (18) found in the small area of RPSC is remarkable. Many species of *Ficus* are very widespread; half of those at La Selva occur also on BCI and at RPSC. The next most diverse genus, *Calathea*

TABLE 1. Characteristics of the species in six families at La Selva.

Taxa	Distribution*	Abundance**	Sexuality***	Habit†	Habitat††
Cyclanthaceae					
Asplundia antioquiae	CR, PA, SA	O	M	E	PF
A. costaricensis	CR, PA	C	M	E	PF
A. euryspatha	CR, PA	O	M	E	PF
A. ferruginea	CR	C	M	E	PF
A. multistaminata	CR	O	M	E	PF
A. sleeperae	CR, PA	O	M	E	PF
A. uncinata	CR	C	M	T	PF
A. vagans	CA, SA	C	M	E	PF
Carludovica rotundifolia	CA	O	M	T	RF
C. sulcata	CR	C	M	T	SU
Cyclanthus bipartitus	CA, SA	C	M	T	SW
Dicranopygium umbrophila	CR	C	M	T	PF
D. wedelii	CR, PA	C	M	T	RF
Evodianthus funifer	CR, PA, SA	C	M	E	PF
Ludovia integrifolia	CR, PA, SA	O	M	E	PF
Sphaeradenia carrilloana	CR	O	M	E	PF
S. pendula	CR	C	M	E	PF
Marantaceae					
Calathea cleistantha	CR, PA	C	H	T	PF
C. cuneata	CR, PA	O	H	T	PF
C. donnell-smithii	CR, PA	R	H	T	RF
C. elegans	CR, PA, SA	O	H	T	PF
C. foliosa	CA	R	H	T	RF
C. gymnocarpa	CR, PA	O	H	T	SU
C. inocephala	CR, PA, SA	O	H	T	SW
C. insignis	CA, SA	O	H	T	SU
C. lasiostachya	CR, PA	C	H	T	PF
C. leucostachys	CR, PA	O	H	T	SW
C. lutea	CA, SA, WI	O	H	T	SU
C. marantifolia	CA, SA	C	H	T	SU
C. micans	CA, SA	C	H	T	ED
C. similis	CR, PA	O	H	T	SU
C. venusta	CR, PA	O	H	T	SW
C. warscewiczii	CR, PA	O	H	T	ED
Ctenanthe villosa	CR	O	H	T	SW
Ischnosiphon elegans	CR	R	H	T	ED
I. inflatus	CR, PA, SA	C	H	T	SW, PF
Pleiostachya pruinosa	CA, SA	O	H	T	SU
P. leiostachya	CA	O	H	T	SW
Cecropiaceae					
Cecropia insignis	CR, PA, SA	O	D	T	ED, SU
C. obtusifolia	CA, SA	C	D	T	SU
Coussapoa nymphaeifolia	CR	O	D	T	ED
C. villosa	CA, SA	O	D	T	ED
Pourouma aspera	CA, SA	O	D	T	PF
P. minor	CR, PA, SA	O	D	T	PF
Clusiaceae					
Calophyllum brasiliense	CA, SA	O	D	T	PF
Clusia cylindrica	CR, PA	C	D	E	PF, ED
C. flava	CA, WI	O	D	E	RF
C. gracilis	CR, PA	C	D	E	PF, ED
C. minor	CA, SA, WI	O	D	E	RF
C. oedematopoidea	CR, PA	O	D	E	PF, RF
C. quadrangula	CA	R	D	E	PF, ED
C. stenophylla	CA	O	D	E	PF
C. uvitana	CR, PA	O	D	E	RF
C. valerii	CR, PA	O	D	E	PF, ED

TABLE 1. Continued.

Taxa	Distribution*	Abundance**	Sexuality***	Habit†	Habitat††
Clusiella elegans	CR, PA, SA	C	D	E	PF
Dystovomita pittieri	CR, PA, SA	O	D	T	PF
Marila laxiflora	CA, SA	R	H	T	RF
Rheedia edulis	CA	O	D	T	PF
Symphonia globulifera	CA, SA, WI	C	H	T	PF
Tovomita weddelliana	CR, PA, SA	R	D	T	PF
Tovomitopsis glauca	CR, PA	C	D	T	RF, PF
T. nicaraguensis	CR, PA, SA	O	D	T	SW, PF
T. silvicola	CR	O	D	T	PF
Vismia bilbergiana	CR, PA, SA	O	H	T	SU
V. macrophylla	CA, SA	R	H	T	SU
V. panamensis	CA	C	H	T	SU
Lauraceae					
Beilschmiedia anay	CA, SA	R	H	T	PF
B. mexicana	CA, SA	R	H	T	PF
Licaria sarapiquensis	CR	O	H	T	PF
L. triandra	CA, WI	O	H	T	PF
L. sp.	CR	R	D	T	RF
Nectandra cissiflora	CR, PA, SA	O	H	T	RF
N. hypoleuca	CR	O	H	T	SU, RF
N. kunthiana	CR, PA, SA	O	D	T	RF
N. membranacea	CR, PA, SA, WI	C	H	T	SU, RF
N. purpurea	CA, SA	O	H	T	RF
N. reticulata	CA, SA	O	H	T	RF
Ocotea atirrensis	CR, PA	C	H	T	RF
O. babosa	CR, SA	O	H	T	RF
O. bijuga	CR, SA	O	H	T	PF
O. caracasana	CR, PA, SA	R	H	T	PF
O. cernua	CA, SA, WI	O	D	T	PF
O. dendrodaphne	CA	C	H	T	PF
O. floribunda	CA, SA, WI	O	D	T	PF
O. hartshorniana	CR, SA	O	H	T	RI
O. ira	CR, PA, SA	O	H	T	PF
O. leucoxylon	CA, SA, WI	O	D	T	PF
O. meziana	CA	C	H	T	PF
O. mollifolia	CR	O	H	T	PF, RF
O. tenera	CR, PA	C	D	T	RF
Persea rigens	CR, PA, SA	R	H	T	PF
Phoebe chavarriana	CR	C	H	T	PF
Moraceae					
Brosimum alicastrum	CA, SA, WI	R	D	T	RF
B. guianense	CA, SA, WI	R	M	T	PF
B. lactescens	CA, SA, WI	O	D	T	PF
Castilla elastica	CA, SA	O	D	T	RF
Clarisia biflora	CA, SA	R	D	T	PF
Dorstenia choconiana	CA	O	M	T	RF, ED
D. contrajerva	CA, SA, WI	R	M	T	RF, SU
Ficus cahuitensis	CR	O	M	E	RF
F. citrifolia	CA, SA	R	M	E	ED
F. colubrinae	CA	O	M	E	RF, ED
F. costaricana	CR, PA, SA	R	M	E	RF
F. crassivenosa	CR	R	M	E	PF
F. donnell-smithii	CA	O	M	E	PF, ED
F. dugandii	CR, PA, SA	R	M	T	PF
F. glaucescens	CA	O	M	T	PF
F. insipida	CA, SA	C	M	T	RF
F. maxima	CA, SA	O	M	T	SW, RF
F. nymphaeifolia	CR, PA, SA	O	M	E	RF
F. pertusa	CA, SA, WI	O	M	E	RF

TABLE 1. Continued.

Taxa	Distribution*	Abundance**	Sexuality***	Habit†	Habitat††
F. popenoei	CA, SA	R	M	E	RF, ED
F. schippii	CR, PA, SA	O	M	E	SW, RF
F. tonduzii	CA, SA	O	M	T	RF
F. velutina	CA, SA	O	M	T	PF
Maquira costaricana	CA, SA	C	D	T	PF, ED
Naucleopsis naga	CA	O	D	T	PF
Perebea angustifolia	CR, PA, SA	C	D	T	PF, ED
Pseudolmedia spuria	CA, WI	R	D	T	PF
Sorocea pubivena	CR, PA	C	D	T	RF, ED
S. trophoides	CR	R	D	T	PF
Trophis involucrata	CR	O	D	T	PF
T. racemosa	CA, SA, WI	O	D	T	RF

* CR = Costa Rica; PA = Panama; CA = Central America; SA = South America; WI = West Indies.
** R = rare, known from one or two individuals; O = occasional, known from three or more distant individuals or small populations; C = common, known from many locations or a few large populations.
*** D = dioecious; M = monoecious; H = hermaphroditic.
† T = terrestrial; E = epiphytic.
†† SU = successional; ED = edges or open areas; SW = swamp; RF = river forest; PF = primary forest.

shares only four species among all three sites. La Selva has the most genera in all the subset families except Marantaceae; *Thalia* and *Stromanthe* (both present on BCI) are absent from La Selva probably because it has very little open swamp habitat. La Selva is relatively depauperate in species only in the Cecropiaceae. Longer histories of disturbance at BCI and RPSC may account for their greater number of species of *Cecropia,* mostly a genus of secondary habitats.

La Selva and RPSC have the same six most diverse genera among the families. BCI shares only the top four genera and has only one species each of *Asplundia* and *Clusia,* both key genera of lowland, wet primary forest. *Cecropia* and *Vismia,* which are characteristic genera of secondary

TABLE 2. Distribution of taxa in six families in three lowland tropical floras, La Selva, BCI, and RPSC.

	La Selva		BCI		RPSC	
Taxa	Genera	Species	Genera	Species	Genera	Species
Cyclanthaceae	8	17	4	5	6	11
Asplundia		8		1		6
Taxa shared			4	2	6	4
Marantaceae	4	21	5	12	4	10
Calathea		16		8		7
Taxa shared			3	6	3	5
Cecropiaceae	3	6	3	7	3	8
Taxa shared			3	3	3	2
Clusiaceae	10	22	9	14	3	7
Clusia		9		1		5
Taxa shared			7	7	2	1
Lauraceae	6	28	4	10	3	12
Nectandra		6		4		5
Ocotea		13		4		6
Taxa shared			4	3	3	6
Moraceae	11	31	11	27	12	30
Ficus		16		17		18
Taxa shared			9	16	8	11
Total taxa	42	125	36	75	31	78
Total taxa shared			30	37	25	29

and moist forest habitats, replace the above two genera within the class of most diverse genera in the subset flora of BCI.

A prediction from these observations about the total number of species expected from La Selva is probably more reliably based on the flora of BCI because these two sites are nearly equal in size, are geographically closer together, and share more genera and species (TABLE 2). If the diversities of the subset floras are representative of their entire floras, then the number of species in the subset can be used to predict the number of species in the entire flora. By this reasoning, La Selva should have a total of 2,200 species. This estimate is similar to an earlier one of 2,000 based mostly on the rate of discovery of additions to the flora (Hammel & Grayum, 1982).

Distribution and Affinities of the Subset Flora

Approximately 13 percent of the species in this study appear to be endemic to Costa Rica (TABLE 1). A large number of these are known only from La Selva. Numerous species described first from wet, mid to low elevation sites in eastern Panama (e.g., Río Guanche in Colón Province and the El Llano–Cartí road in Panamá and San Blas provinces) are now known from La Selva. Conversely, species previously known only from La Selva are now being found in these same areas of Panama, intervening areas, and nearby Nicaragua (Grayum; pers. comm.; Stevens, pers. comm.; pers. obs.). It is likely that many of these same species will be found in northern South America as well (Gentry, 1982b).

In his introduction to the Flora of Costa Rica Standley (1937) pointed out the relationship of the Costa Rican flora to that of South America. For each of his floristic regions Standley noted that the greatest influence was from South America. Gentry (1978, 1982b) has pointed out that new collections from middle and eastern Panama are beginning to reveal more species common to the wet lowlands of both Central and South America. The La Selva flora has already given evidence of the extension of this pattern into Costa Rica (Hammel & Grayum, 1982). Thus, it should come as no surprise that 85 percent of the species in the subset flora of La Selva are known also from Panama or South America. Of those, 45 percent are widespread in the neotropics. Most significantly, about 20 percent of the species in these six families are known only from Panama and Costa Rica, and another 20 percent reach from South America north only as far as Costa Rica. Only two species, *Clusia flava* and *Naucleopsis naga,* find their southern limit in Costa Rica. The distribution of species of the subset flora clearly suggests that La Selva has more in common with areas to the south than with the north.

The distribution of closely related species provides a more precise basis for discussion of the affinities of a particular flora. Familiarity with the families and a review of the literature suggested a possible sister species for about 50 percent of the 123 species. Of these, 44 percent occur in Panama or South America, 9 percent are restricted to areas north of Costa Rica, and 10 percent occur in Costa Rica but are isolated by elevation or mountain barriers. The rest are widespread and sympatric with their presumed sister species. These distribution patterns again demonstrate that the principal phytogeographic affinities of La Selva lie to the south.

CONCLUSION

Although the 123 species in six families here analyzed comprise less than 10 percent of the total, their characteristics are, for the most part, representative of the entire flora of La Selva. Because most of them occur in primary or riverine forest they are probably also representative of the original forest of the wet Caribbean lowlands of southern Central America. Intensive studies of this sort (i.e., florulas of the wet lowland tropics) typically reveal numerous new and presumably endemic species, but they also, without fail, extend the range of species formerly thought endemic to other areas. In the case of La Selva and for the Caribbean lowlands in general the other areas lie to the south. Both in the distribution of species and the distribution of closely related species this subset of the flora demonstrates the southern phytogeographic affinities of La Selva.

ACKNOWLEDGMENTS

I would like to thank K. Bawa, A. Gentry, and J. Trainer for many helpful comments on an earlier version of this manuscript. I appreciate the use of facilities and loan of specimens from the following herbaria: C, CR, DUKE, F, GH, K, LL, MICH, MO, NY and US. The fieldwork, which formed the basis of a Ph.D. dissertation, was supported by a research assistantship from Duke University funded by an NSF grant (DEB 79-04417) to D. E. Stone and R. L. Wilbur. I also gratefully acknowledge support from an OTS Fellowship funded through the Noyes Foundation.

LITERATURE CITED

BAWA, K. S. 1980. Evolution and dioecy in flowering plants. Ann. Rev. Ecol. and Syst. 11: 15–39.

——— AND J. E. CRISP. 1980. Wind-pollination in the understory of a rain forest in Costa Rica. J. Ecol. 68: 871–876.

———, D. R. PERRY, AND J. H. BEACH. 1985. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility systems. Amer. J. Bot. 72: 331–345.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford.

DODSON, C. AND A. H. GENTRY. 1978. Flora of the Río Palenque Science Center. Selbyana 4: 1–628.

GENTRY, A. H. 1978. Floristic knowledge and needs in Pacific tropical America. Brittonia 30: 134–153.

———. 1982a. Patterns of neotropical plant species diversity. Pp. 1–84 *in* M. K. HECHT, B. WALLACE, AND G. T. PRANCE, eds., Evolutionary biology. Plenum Press, New York.

———. 1982b. Phytogeographic patterns as evidence for a Chocó refuge. Pp. 112–136 *in* G. PRANCE, ed., Biological diversification in the tropics. Columbia Univ. Press, New York.

GIVNISH, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. Evolution 34: 959–972.

HAMMEL, B. E. 1984. Systematic treatment of the Cyclanthaceae, Marantaceae, Cecropiaceae, Clusiaceae, Lauraceae, and Moraceae for the flora of a wet lowland tropical forest, Finca La Selva, Costa Rica. Ph.D. dissertation, Duke Univ., Durham.

——— AND M. H. GRAYUM. 1982. A preliminary report on the flora of La Selva Field Station. Ann. Missouri Bot. Gard. 69: 420–425.

HARTSHORN, G. S. 1983. Plants: introduction. Pp. 118–183 *in* D. H. JANZEN, ed., Costa Rican natural history. Univ. Chicago Press, Chicago.

STANDLEY, P. C. 1937. Flora of Costa Rica. Field Mus. Nat. Hist., Bot. Ser. 18: 5–63.